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# SKULL AND RELATIONSHIPS OF THE UPPER JURASSIC SAUROPOD *APATOSAURUS* (REPTILIA, SAURISCHIA)

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# ABSTRACT

Evidence is presented to show that 1) *Apatosaurus* probably possessed a *Diplodocus*-like, rather than *Camarasaurus*-like, skull, and 2) *Apatosaurus* and *Diplodocus* are closely related and well separated from *Camarasaurus*. A *Diplodocus*-like skull attributed to *Apatosaurus* by W. J. Holland over a half century ago is described for the first time. A cranium and a pair of quadrates that are very similar to those of *Diplodocus* are also described and shown probably to belong to *Apatosaurus*. Inaccuracies and omissions in previous descriptions of the skull of *Diplodocus* have necessitated a redescription of much of its external features and braincase. Differences between the skull attributed here to *Apatosaurus* and that of *Diplodocus* are of a subtle proportional and structural nature. Comparisons of the postcranial skeletons of the Jurassic *Apatosaurus*, *Diplodocus*, and *Camarasaurus* demonstrate that the former two genera share a large number of significant features and are quite distinct from the latter.

*Apatosaurus* and *Diplodocus*, along with the Jurassic *Barosaurus*, *Cetiosauriscus*, *Mamenchisaurus*, and *Dicraeosaurus* and the Cretaceous *Nemegtosaurus*, should be grouped under Diplodocidae Marsh, 1884.

# INTRODUCTION

Of the six well-established sauropod genera from the Upper Jurassic Morrison Formation of North America, *Brachiosaurus*, *Haplocanthosaurus*, and *Barosaurus* are rare and the latter two incompletely known. The other three, *Camarasaurus*, (=*Morosaurus*, =*Uintasaurus*), *Apatosaurus* (=*Brontosaurus*), and *Diplodocus* are common and well known. The last three genera were described a century ago on small but diagnostic portions of skeletons (Cope, 1877*a*; Marsh, 1877*b*, 1878*a*). Although large collections of numerous isolated elements and some partial skeletons of *Camarasaurus*, *Apatosaurus*, and *Diplodocus* were made during the next quarter century, adding greatly to the knowledge of these genera, significant misinterpretations concerning their morphology and relationships arose. Despite detailed descriptions (Gilmore, 1925, 1936; Hatcher, 1901*a*, 1903*b*; Holland, 1906) of excellent specimens of all three genera even after this period, some of the misinterpretations were so entrenched in the literature that they persist today. The misunderstandings discussed here regard two important aspects of the morphology and relationships of *Apatosaurus*. First, since the original restorations of "*Brontosaurus*" published by Marsh (1883, 1891), the skull of *Apatosaurus* has been incorrectly depicted as being *Camarasaurus*-like and the alternative suggestion presented by Holland (1915*a*) and supported here, that it is *Diplodocus*-like, has been almost totally ignored. Second, *Apatosaurus* has been falsely viewed as more closely related to *Camarasaurus* than to *Diplodocus*, despite the fact that descriptions of their postcranial skeletons demonstrate just the opposite.

In an earlier review of the nature of the skull of *Apatosaurus*, we (McIntosh and Berman, 1975) discussed the controversy raised by Holland (1915*a*, 1924), who refuted Marsh's (1883, 1891) use of probable *Camarasaurus* skulls in his restorations of *Apatosaurus*, pointing out that the skulls were not found directly, or even closely, associated with postcranial skeletons of this genus. Holland argued that the skull of *Apatosaurus* is probably like that of *Diplodocus*. His opinion was based almost solely on a very large *Diplodocus*-like skull that was very closely associated with two nearly perfectly preserved postcranial skeletons of *Apatosaurus* in the quarry at what is now Dinosaur National Monument near Jensen, Utah. This skull was never described by Holland and his assertion was almost totally disregarded, because it ran counter to the then well-established view that *Apatosaurus* is structurally more similar and more closely related to *Camarasaurus* than to *Diplodocus*; this skull is described here for the first time. A pair of quadrates and the greater portion of a cranium that are nearly indistinguishable from those of *Diplodocus* are also described as probably belonging to *Apatosaurus*. These elements were found near Morrison, Colorado, by Marsh's collectors in 1877 and evidence is presented that suggests that they belong to the holotype of *A. ajax*. Previous descriptions of the skull of *Diplodocus* are inaccurate and incomplete, necessitating a redescription of most of its external features and braincase. A comparison of the postcranial skeletons of the three common, Morrison Formation sauropods confirms that *Apatosaurus* and *Diplodocus* are very similar and are distinct from *Camarasaurus*.

The close resemblance of the skull and postcranial skeleton of *Apatosaurus* to those of *Diplodocus* clearly indicates that *Apatosaurus* is more closely related to *Diplodocus* than to *Camarasaurus*. *Apatosaurus* and *Diplodocus*, along with five lesser known genera, *Barosaurus*, *Cetiosauriscus*, *Mamenchisaurus*, *Dicraeosaurus*, and *Nemegtosaurus*, are grouped under Diplodocidae Marsh, 1884, for the first time.

## ABBREVIATIONS

AMNH, CM, USNM, and YPM refer to collections at the American Museum of Natural History, the Carnegie Museum of Natural History, the National Museum of Natural History, and the Yale Peabody Museum, respectively.

Abbreviations used in figures are as follows:

| | |
|---|---|
| aca | canal for anterior cerebral artery |
| Bo | basioccipital |
| bpp | basipterygoid process |
| Bs | basisphenoid |
| ca | crista antotica |
| cp | crista proötica |
| Eo | exoccipital |
| F | frontal |
| gr pn | groove for palatine branch of facial nerve |
| ica | foramen for internal carotid artery |
| J | jugal |
| jv | foramen for jugular vein |
| L | lacrimal |
| Ls | laterosphenoid |
| M | maxilla |
| mpa | canal for median palatine artery |
| N | nasal |
| Op | opisthotic |
| Os | orbitosphenoid |
| P | parietal |
| pa | foramen for palatine artery |
| pao | preantorbital opening |
| Pf | prefrontal |
| pf | posttemporal fenestra |
| Pm | premaxilla |
| pn | foramen for palatine branch of facial nerve |
| Po | postorbital |
| Pr | proötic |
| Ps | parasphenoid |
| Pt | pterygoid |
| Q | quadrate |
| Qj | quadratojugal |
| So | supraoccipital |
| Sq | squamosal |
| s-Sq | sutural surface for squamosal |
| I–XII | foramina for cranial nerves |

## HISTORICAL REVIEW

### Previous Collections and Descriptions

In order to understand fully and, therefore, hopefully, to resolve remaining areas of confusion concerning the morphology of *Apatosaurus* and its relationships to other sauropods, particularly to *Camarasaurus* and *Diplodocus*, it is necessary to give a detailed chronicle of the circumstances and events surrounding the collecting and description of those specimens pertinent to this topic.

In July, 1877, Marsh (1877*a*) described a large incomplete sauropod sacrum (YPM 1835) as *Titanosaurus montanus*, which was found by Arthur Lakes and H. C. Beckwith at what was later designated as YPM quarry 1 north of Morrison, Colorado (Ostrum and McIntosh, 1966). As Lydekker (1877) had used the same generic name several months earlier in describing two caudals and a chevron of a different species of sauropod, *Titanosaurus indicus*, Marsh (1877*b*) altered the name of his Morrison specimen to *Atlantosaurus montanus* in December of the same year. Farther on in the same publication Marsh also described a second sauropod sacrum and vertebrae as representing a new genus, *Apatosaurus ajax*. This specimen, also discovered by Lakes in another quarry near Morrison, later designated YPM quarry 10, had originally been sent to E. D. Cope for identification. However, when Marsh purchased the specimen from Lakes, Cope sent it to the Yale Peabody Museum at Lake's request. Marsh kept accurate records of his collections and an accession number was placed on all fossils arriving at the museum as the boxes containing them were unpacked. Later, when the bones were identified and studied, they were given a catalogue number. The *Apatosaurus* sacrum from YPM quarry 10 which originally had been sent to Cope, was included as part of accession no. 993 and was later catalogued as YPM 1860. Lakes was to make a number of additional shipments from a total of 11 separate quarries at Morrison. In the shipments that followed from quarry 10 there was a very large femur that was attributed by Marsh (1878*a*) to a new species of *Atlantosaurus*, *A. immanis*, and was later catalogued as YPM 1840. The numerous shipments from Morrison included many more elements from quarry 10. By 1883 the Morrison collections had been prepared and it was evident that the material from quarry 10 belonged to two very large skeletons. The smaller of the two, which included the *Apatosaurus ajax* sacrum YPM 1860, was from a dark clay layer that imparted a black color to it. The larger skeleton, which included the *Atlantosaurus immanis* femur YPM 1840, came from a light colored sandstone immediately overlying the clay layer and its elements are light colored. S. W. Williston, who, as Marsh's assistant, sorted out the bones of these two specimens in 1883, noted in a memorandum to Marsh their close similarity and believed them to belong to the same species.

Included in the shipments from Morrison were cranial materials that have a direct bearing on the controversy about the nature of the skull of *Apatosaurus*. The second Morrison shipment sent by Lakes and B. F. Mudge in 1877 and assigned accession no. 1002 contained material from quarries 1, 8, and 10. Among this material was the greater part of a cranium on which was originally marked only the accession number. The importance of this specimen was apparently not realized at the time of its receipt, because the box number, which would have indicated from which of the three quarries it came, was not recorded on the cranium. In sorting out the collections from Morrison, Williston assigned the cranium to the "*Atlantosaurus immanis*" specimen, indicating that he believed it was found in quarry 10. Marsh (1896) later figured the cranium as *Atlantosaurus montanus*, which would appear to indicate that he believed it to be from quarry 1. The cranium, as will be shown in a later section, is *Diplodocus*-like in structure and its quarry origin is, therefore, of great importance. Adding to the confusion, when the quarry 10 material was catalogued the number YPM 1860 was placed on not only the bones of the holotype of *Apatosaurus ajax*, but also on those of "*Atlantosaurus immanis*." It is not known why, when or by whom this was done. Also from quarry 10 at Morrison was a pair of very large *Diplodocus*-like quadrates. Although the catalogue number YPM 1860 is marked on both, only the left one bears the accession no. 1052 and the box no. 53, which definitely identifies its origin as quarry 10. The quadrates, therefore, provide important evidence on the nature of the skull of *Apatosaurus*.

In the summer of 1879 two of Marsh's foremost collectors, W. H. Reed and E. G. Ashley, discovered the major portions of two very large sauropod skeletons in the same stratum of two adjacent quarries at Como Bluff, Wyoming. These were described by Marsh as two species of a new genus, *Brontosaurus*. The more perfect skeleton, YPM 1980 from Como Bluff quarry 10 (to date, one of the most complete sauropod skeletons ever found), he described (1879*a*) as the holotype of the type species *Brontosaurus excelsus*, whereas the other, YPM 1981, from Como Bluff quarry 11, he described (1881) as the type of *B. amplus*. YPM 1980 lacked the skull, first few cervicals, posterior half of the tail, ulna, and all the bones of both the manus and pes except the astragalus; YPM 1981 possessed only one bone not represented in YPM 1980, the second metacarpal. In 1883 Marsh published a restoration of *B. excelsus*, the first for any sauropod dinosaur. Though his restoration was quite good overall, it contained numerous errors, most of which depicted "*Brontosaurus*" as having *Camarasaurus*-like features. The feet were incorrectly restored with a full complement of phalanges and, in *Camarasaurus* fashion, two proximal carpals and tarsals were attributed to "*Brontosaurus*"; *Apatosaurus* has only one each of these elements, the astragalus and "scapholunar." The crushed ulna and manus used in Marsh's restoration belonged to a partial skeleton of a large adult *Camarasaurus*, YPM 4633, from YPM Como Bluff quarry 1A. Detailed drawings of these elements, which were prepared for Marsh for a proposed sauropod monograph, have been reproduced by Ostrom and McIntosh (1966). The narrow, elongated metacarpals and the slender ulna of YPM 4633 are in sharp contrast to the short, stout metacarpals and the extremely robust ulna of *Apatosaurus*. When YPM 1980 was mounted at the Yale Peabody Museum the ulna and manus of YPM 4633 were used to complete the skeleton. Marsh was unaware of the correct number of cervical and caudal vertebrae of "*Brontosaurus*" and restored the neck and tail after "*Morosaurus*," that is, *Camarasaurus*, with too few vertebrae. The neck was shown as having only 12 vertebrae as in *Camarasaurus*, rather than the correct number of 15. Marsh also did not know that "*Brontosaurus*" had a long, "whip-lash" tail, containing as many as 82 vertebrae, almost twice the number found in *Camarasaurus*. Most importantly, for the missing skull of his restoration of YPM 1980 Marsh used a large, incomplete *Camarasuarus*-like skull, YPM 1911, from YPM Como Bluff quarry 13, located about 4 mi from and in a stratum distinctly lower than that of YPM quarry 10 from which came "*B.*" *excelsus* (Ostrom and McIntosh, 1966). Quarry 13 had yielded four partial skeletons of *Camarasaurus*, including the type of "*Morosaurus*" *lentus* (YPM 1910), and a quadratojugal and caudal centrum of *Diplodocus*, but no identifiable remains of *Apatosaurus*. The skull YPM 1911 consists of premaxillae, maxillae, lacrimals, vomers, dentaries, loose teeth, and some fragments; its massive jaws and spatulate teeth are prominent *Camarasaurus* features. In 1891 Marsh published a revised reconstruction of "*Brontosaurus*," which was in some ways less accurate than his first (Riggs, 1903*a*). Although he added a thirteenth vertebra to the cervical series, he also increased the number of dorsals from the correct 10 to 14, which is closer to the 12 possessed by *Camarasaurus*. In his second restoration Marsh used a different skull, USNM 5730, from YPM-USNM Canyon City quarry 1 at Garden Park, Colorado. It is about the same size as the skull YPM 1911 but somewhat more complete, consisting of maxillae, premaxillae, squamosal, dentaries, cranium, and perhaps a quadrate. USNM 5730 also has the distinctive massive jaws and spatulate teeth of *Camarasaurus*. The skull was found isolated from other skeletal materials in quarry 1, representing as many as five or six sauropod genera. Although *Apatosaurus* was one of those genera present, quarry maps indicate no reason to believe that the skull was associated with any remains of this genus.

Most, if not all, of the vast collections of sauropods made by the American Museum of Natural History from 1897 to 1905 at Bone Cabin quarry, Como Bluff, and nearby localities in southeastern Wyoming, belonged to the three common genera of the Morrison Formation. A partial skeleton of *Apatosaurus* from Como Bluff was described by Osborn (1898) as *Camarasaurus* and, although not explicitly stated, he strongly implied that *Camarasaurus* and "*Brontosaurus*" were very closely related, if not synonymous. The greater part of the collections from Bone Cabin quarry consisted of limbs, feet, and tail segments. The feet were sometimes articulated with the limbs, but more often not. For unknown reasons the numerous undersized limbs were separated out as "*Morosaurus*," the large robust limbs as "*Brontosaurus*" and the large slender limbs as *Diplodocus;* these assignments caused problems. The robust hindlimb bones of *Camarasaurus* are very similar to those of *Apatosaurus* and some of the large hindlimb elements of the former were assigned to the latter. Also resulting in misidentifications, the forelimb bones of *Camarasaurus* are slender and the radius and ulna, in particular, resemble those of *Diplodocus*. Further, it was not known that the metacarpals of *Camarasaurus* were much longer and more slender than those of *Diplodocus*. Important to the discussion here was the misidentification of a right radius, ulna and manus of *Camarasaurus* AMNH 965 from Bone Cabin quarry. Osborn (1904) originally described the manus correctly as "*Morosaurus*" but apparently reconsidered his identification about a year later when he sent a cast of it to the Carnegie Museum in response to their request for a manus to complete the *Diplodocus* being mounted there. A reduced model of the manus was not only used in the Carnegie Museum exhibit, but also in 10 casts of the entire skeleton sent to museums throughout the world. Osborn also sent photographs of AMNH 965 to Abel, who not only published them (1910) as the manus of *Diplodocus*, but also used them in his restoration of this genus. Forelimbs of *Diplodocus* and forefeet of *Camarasaurus* from Bone Cabin quarry were also mistakenly associated as composite specimens of *Diplodocus* and sent by the American Museum of Natural History to a number of museums throughout the world.

In the early 1900s numerous important discoveries were made that revealed errors in Marsh's (1883, 1891) restorations of *Apatosaurus*. Most significantly, these discoveries not only removed some of the erroneous resemblances between *Camarasaurus* and *Apatosaurus* that were suggested by Marsh's restorations of the latter, but also disclosed some important features shared by *Apatosaurus* and *Diplodocus*. Hatcher (1901*b*, 1902) described the forelimb and, more importantly, the forefoot of *Apatosaurus* correctly, using associated material, CM 563, now mounted at the University of Wyoming, Laramie. Hatcher, however, failed to notice that the forefeet of *Apatosaurus* and *Diplodocus* are much closer in structure than either is to that of *Camarasaurus*. Riggs (1903*b*) not only showed that *Brontosaurus* is a junior synonym of *Apatosaurus*, but also demonstrated that *Apatosaurus* possesses 10 dorsal vertebrae, that the number of sacral vertebrae of sauropods is not a valid generic character as Marsh believed, and that the chevrons of the midcaudals of *Apatosaurus* are *Diplodocus*-like in having fore and aft distal processes. Undoubtedly, the most important event with regard to this discussion here was the discovery in 1909 by Earl Douglass of the Carnegie Museum of the well-known, richly fossiliferous, dinosaur quarry at what is now Dinosaur National Monument, near Jensen, Utah. The first specimen discovered and excavated from this quarry, known then as Carnegie quarry, was important not only in being the most complete *Apatosaurus* skeleton ever found, but in having a large skull closely associated with it. In 1915 Holland (1915*b*) not only described the postcranial skeleton, CM 3018, as a new species, *A. louisae*, but, on the basis of the skull associated with it, he (1915*a*) also challenged Marsh's (1883, 1891) original identifications of the skull of "*Brontosaurus*." The type of *A. louisae,* which was designated field no. 1, was found (Fig. 1) largely articulated, but with the trunk, neck and forelimb somewhat displaced. A second, almost as complete and articulated skeleton of this species, field no. 40, lay beside CM 3018 and, although an adult specimen, was 15 to 20% smaller than the type; this specimen is now at the Los Angeles County Museum. Lying beside cervicals 12 and 13 of field no. 40 and about 4 m from the atlas of CM 3018 was a large *Diplodocus*-like skull without mandibles, CM 11162. Though the posterior portion of a medium-sized *Diplodocus* skeleton (field no. 60) lay only about 3 m from the skull CM 11162 (Fig. 1), their size difference precludes any possibility that they were associated. Noting the close proximity of the skull CM 11162 to the skeleton CM 3018, their position in the same layer and the exact fit of the occipital condyle of the skull into the articular cup of the atlas of CM 3018, Holland (1915*a*:274) concluded that the *Diplodocus*-like skull represented the true skull of *Apatosaurus,* stating that "Had nothing in the past been written in reference to the structure of the skull of *Brontosaurus* the conclusion would naturally and almost inevitably have been reached that this skull belongs to the skeleton the remainder of which has been recovered." However, when the skeleton of *A. louisae* CM 3018 was mounted at the Carnegie Museum, Holland considered using this skull but refrained from doing so apparently at the insistence of Osborn (Holland, 1915*a*) and, instead, the skeleton stood headless for more than 20 years (Gilmore, 1936). After Holland's death in 1932 a cast of the *Camarasaurus* skull CM 12020 was used to complete the mount. This large, incomplete skull was collected at Carnegie quarry as part of field no. 240, which included the greater part of an adult *Camarasaurus* skeleton, and originally both the skull and postcranial skeleton received the same catalogue number, CM 11393. There is no reason to believe that the skull and postcranial skeleton did not belong to the same individual and, further, no *Apatosaurus* material was found nearby to suggest that the skull might pertain to this genus. It is also important to mention here that Holland (1915*a*) described a second feature of *Apatosaurus* that further helps to substantiate its closeness in structure to *Diplodocus*, the presence of a "whip-lash" type of tail. This structure was clearly documented not only in *A. louisae* CM 3018, but in a medium-sized specimen, CM 3378, found isolated at the far western end of Carnegie quarry and consisting of a vertebral column complete and articulated from the mid-cervical region to the eighty-second caudal.

Three other specimens found closely associated at Carnegie quarry (Fig. 1) are pertinent to this discussion. A partial skeleton, field no. 24, of a small, juvenile *Apatosaurus,* CM 3390, was found lying near the cervicals of *A. louisae* CM 3018. CM 3390 consists of the complete dorsal vertebral series, sacrum, caudals 1–12, left pelvic bones, right ischium, and a few ribs. Earl Douglass, who directed the Carnegie quarry excavation, estimated its total length to be about 5 m. Most interesting, however, in the records of the collection from the quarry Douglass states that "About 20 feet east of here [field no. 24], ten or more connected cervicals of a small dinosaur (field no. 37) were found, also the anterior portion of a small jaw with pencil-like teeth (field no. 35). I worked out nos. 24 and 37 later when in the museum in Pittsburg and this confirmed the surmise that these belonged to the same individual." If these three specimens belonged to the same individual, then the *Diplodocus*-like teeth of the jaw provides additional evidence on the nature of the skull of *Apatosaurus*.

Carnegie quarry has also been important in yielding excellent skulls of *Diplodocus;* two of these are relied on heavily in redescribing the skull of *Diplodocus* in a later section. The complete and uncrushed skull and mandible CM 11161 was discovered beside the anterior caudals of the nearly complete vertebral column of the medium-sized *Apatosaurus* CM 3378 found isolated at the far western end of the quarry. Earl Douglass viewed this association as evidence that *Apatosaurus* possessed a *Diplodocus*-like skull (McIntosh and Berman, 1975). The skull, however, was the basis of Holland's (1924) description of the skull of *Diplodocus*. The palate and lower jaw of CM 11161 were

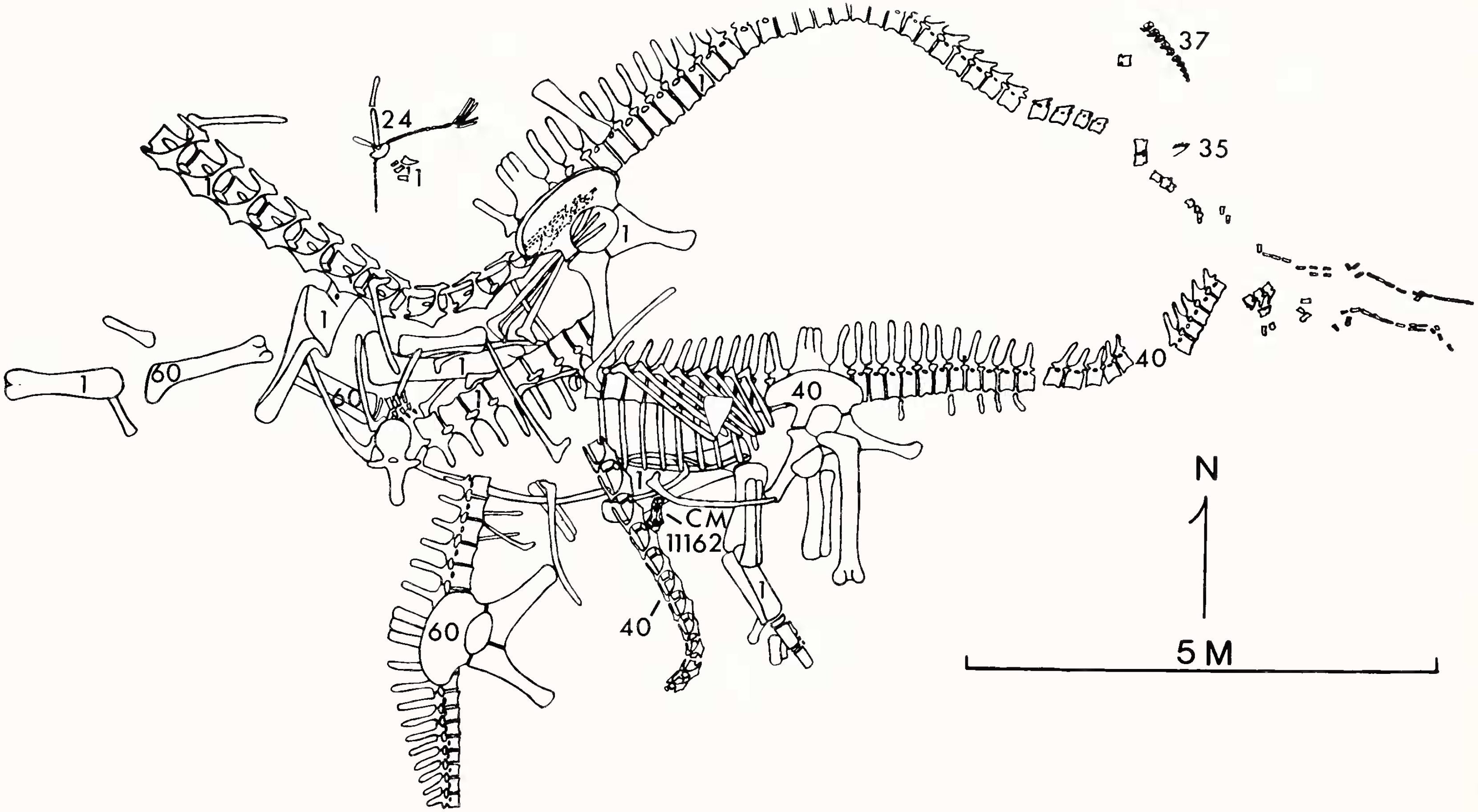

Fig. 1.—Relative quarry positions of various sauropod specimens discussed in text from Dinosaur National Monument. Redrawn from quarry map on file at Carnegie Museum of Natural History showing specimens removed from quarry by that institution. Field nos. 1 and 40, postcranial skeletons of type of *Apatosaurus louisae*, CM 3018, and specimen now at the Los Angeles County Museum; CM 11162, skull very probably belonging to field no. 1 or 40; field no. 60, postcranial skeleton of *Diplodocus;* field no. 24, portion of postcranial skeleton of a juvenile *Apatosaurus* (CM 3390), field no. 37, series of cervical vertebrae, and field no. 35, anterior portion of small jaw with *Diplodocus*-like teeth, probably belonging to one individual of *Apatosaurus*.

recently redescribed (McIntosh and Berman, 1975). CM 3452, consisting of skull, mandible, and the first six cervicals in articulation, is a very important specimen in that it is the only instance in which a *Diplodocus* skull has been found articulated with postcranial elements. This specimen was sketchily illustrated and briefly referred to a few times by Holland (1924) in his description of the skull of *Diplodocus*. Some of its disarticulated palatal bones were recently described (McIntosh and Berman, 1975).

### DISCUSSION

Numerous factors can be attributed to the origin of the false notions that *Apatosaurus* possessed a *Camarasaurus*-like skull and was more closely related to *Camarasaurus* than to *Diplodocus*. Not least among these is that the first descriptions of *Apatosaurus* Marsh (1877*b*) and *Camarasaurus* Cope (1877*a*) were based on only very small portions of the type skeletons, were very brief, and were without illustrations. The reason for this was the Cope-Marsh feud at that time (Romer, 1964). In their zeal to be first in describing the large sauropods of North America, Marsh and Cope rushed out descriptions on the first few elements of the type skeletons they received from their collectors, even though the greater portions of the skeletons were still being excavated. During the next year and a half, as more material was collected and prepared, these descriptions were only slightly amplified (Cope, 1877*c*, 1878*a*; Marsh, 1879*b*), including figures of a few bones of both genera, but neither genus received the description it merited. Thereafter, both genera were largely ignored. Marsh's (1878*b*, 1879*a*) descriptions of two new sauropods, *Morosaurus* and *Brontosaurus*, further complicated the picture. Both genera were based on good material and were described in detail with many excellent illustrations. However, of the half dozen or more partial skeletons Marsh had identified as *Morosaurus*, all were juveniles or subadults and were considerably smaller than the two large skeletons of *Brontosaurus* he had. As a result, the few adults *Camarasaurus* specimens he had were apparently misidentified as *Brontosaurus* because of their large size. Had he realized that "*Monosaurus*" attained the same size as "*Brontosaurus*," he might not have used the large *Camarasaurus*-like skulls YPM 1911 and USNM 5730, and the ulna and manus of the partial skeleton of the adult *Camarasaurus* YPM 4633 in his (1883, 1891) restorations of *Brontosaurus*. Although YPM 1911 and USNM 5730 represent individuals much larger than any of the specimens in Marsh's collection, which he recognized as *Morosaurus*, they are not too large when compared with the type skeleton of *C. supremus* described by Cope (1877*a*), for which he did not report any skull parts (portions of the skull, including upper and lower jaws with teeth, were later described by Osborn and Mook, 1921). It can also be pointed out that Marsh never indicated his use of referred specimens, seemingly selected on purely conjectural grounds, to complete his restorations of *Brontosaurus*. This practice undoubtedly helped to perpetuate many of the misconceptions about the structure of *Apatosaurus*. Adding to the confusion, in 1898 Osborn described a "*Brontosaurus*" skeleton as *Camarasaurus*, apparently believing the two genera to be synonymous. Even after a thorough study of the type of *Camarasaurus* by Osborn and Mook (1921) showed it to be a senior synonym of *Morosaurus*, the erroneous concept of a close relationship between *Camarasaurus* and *Apatosaurus* persisted. This was due largely to 1) the recognition that the skeletons of *Apatosaurus* and *Camarasaurus* are very robustly constructed and their hindlimbs are nearly indistinguishable, whereas the skeleton of *Diplodocus* is very slender in structure and its hindlimbs are easily identified and 2) the continued acceptance of the false notion that *Apatosaurus* possessed a *Camarasaurus*-like skull. It is remarkable that Holland's claim that *Apatosaurus* possessed a *Diplodocus*-like skull continued to fail to receive serious consideration even after accurate restorations of the postcranial skeletons of *Apatosaurus* (Gilmore, 1936), *Camarasaurus* (Gilmore, 1925) and *Diplodocus* (Hatcher, 1901*a*, 1903*b*; Holland, 1906) became available. Despite the fact that even a cursory comparison of their postcranial skeletons, excepting their hindlimbs, shows that *Apatosaurus* is not only quite distinct from *Camarasaurus*, but shares a great number of significant features with *Diplodocus*, such observations have, to date, not been made.

Examination of the type skeletons of *Apatosaurus ajax* YPM 1860 and *Atlantosaurus immanis* YPM 1840, the only postcranial specimens from YPM quarry 10 at Morrison, Colorado, substantiates Williston's observation that they belong to the same species and the latter is considered to be a junior synonym of *A. ajax*. The pair of *Diplodocus*-like quadrates from YPM quarry 10 are identical in size, color and morphological detail, leaving almost no doubt they belong to the same individual. Further, their black color suggests that they belong to the identically colored skeleton YPM 1860, rather than to the light colored skeleton YPM 1840. The greater portion of cranium contained in the shipment of specimens Marsh received from Lakes and Mudge in 1877 from the Morrison quarries 1, 8, and 10 is also *Diplodocus*-like and is also thought to belong to YPM 1860. If the cranium is from quarry 10, as Williston must have thought in assigning it to *Atlantosaurus immanis* YPM 1840, then it probably belongs to YPM 1860, because both have the same black coloring. It is also important to point out that the quadrates and the partial cranium are of the appropriate sizes to have belonged not only to the same animal, but to a skeleton the size of YPM 1860 or YPM 1840. The other possible, but far less likely, origin of the cranium is YPM quarry 1, as Marsh (1896) apparently thought when describing it as *Atlantosaurus montanus*. In addition to the type sacrum YPM 1835 of *A. montanus,* YPM quarry 1 has yielded *Camarasaurus*-like vertebrae. Examination of the sacrum YPM 1835 reveals that it is too fragmentary to permit generic identification and it could conceivably belong to either *Apatosaurus, Diplodocus,* or *Camarasaurus,* which have been found at the 11 quarries at Morrison. It is not unlikely, however, that either Williston or Marsh may have obtained more precise locality information for the cranium from Lakes or Mudge well after it arrived at the Yale Peabody Museum and that this was never recorded in the catalogues. The cranium now bears the catalogue number YPM 1860, but we do not know when, by whom, or on what basis it was given this number. It is possible that this was done at the same time that this number was placed on the bones of both the type of *Apatosaurus ajax* and "*Atlantosaurus immanis*" (=*A. ajax*) YPM 1840. White (1958), on the basis of the catalogue number YPM 1860 on the cranium, quite reasonably assumed that it was part of the type of *A. ajax* and that Marsh (1896) had a *lapsus calami* in describing it as *Altantosaurus montanus*. Further, White considered the cranium to closely resemble that of *Camarasaurus* and, therefore, to provide evidence of a close relationship between *Apatosaurus* and *Camarasaurus*. It is surprising that White appears not to have been aware of the pair of quadrates from YPM quarry 10; had he examined them, he surely would have immediately recognized their *Diplodocus*-like structure and so might have noticed the *Diplodocus*-like nature of the cranium. White also mentioned that parts of both pterygoids, which embrace the recesses basipterygoideus, are present with the cranium. We found one of these elements but were unable to either confirm or give an alternative to his identification.

The probable *Apatosaurus* skull CM 11162 has never been described and only a small portion of it has been illustrated. In a discussion of tooth replacement in *Diplodocus,* Holland (1924:Fig. 5) illustrated a small part of the anterior end of the right maxilla, where, due to the loss of surface bone, the replacement pattern is clearly seen. Additional preparation of CM 11162 has revealed considerable plaster restoration. Further, the Carnegie Museum of Natural History collections include a plaster cast of the skull in its restored state and it is suspected that the restoration and cast were done at the request of Holland, who (1915*a*:277) stated that at times he was inclined to mount it on the postcranial skeleton of *A. louisae* CM 3018 on exhibit at Carnegie Museum. After a thorough review of all the evidence we (McIntosh and Berman, 1975) concurred with Holland that the skull CM 11162 probably represents *Apatosaurus,* if not the type of *A. louisae*.

## SKULL OF *DIPLODOCUS*

The skull here described as probably belonging to *Apatosaurus*, CM 11162, is so close to that of *Diplodocus* in structure that the problem of distinguishing between them is difficult. In light of this problem, comparisons using previous descriptions of skulls of *Diplodocus* are made somewhat tenuous, because these skulls were found isolated, leaving some doubt as to their identification. Most importantly, previous descriptions of the skull of *Diplodocus* are incomplete and contain numerous inaccuracies. The *Diplodocus* skull CM 3452 from Dinosaur National Monument is, therefore, emphasized here, because it represents the only known direct association of skull and postcranial skeleton of this genus. In Holland's (1924:Pl. XL, fig. 2) illustration of this specimen only the damaged and partially disarticulated right side of the skull is shown. Further preparation reveals that the left side, occiput, and roof of the skull are nearly perfectly preserved. The essentially complete and uncrushed skull CM 11161 is here considered to represent *Diplodocus* even though it was found closely associated with the nearly complete vertebral column of *Apatosaurus* CM 3378 isolated at the far western end of Dinosaur National Monument quarry. This assignment is justified by the common possession of characters of CM 11161 and the unquestionable *Diplodocus* skull CM 3452 that are not seen in the probable *Apatosaurus* skull CM 11162. An excellently preserved cranium, CM 26552 from Dinosaur National Monument, on which our description of the braincase of *Diplodocus* mainly rests, is assigned to this genus on the same grounds; CM 26552 has not been previously described. Similarly, the posterior portions of the skulls CM 662 used by Holland (1906) and AMNH 694 by Osborn (1912) to describe the braincase of *Diplodocus* exhibit a closer resemblance to CM 3452 than to CM 11162. The skulls USNM 2672 and USNM 2673 used by Marsh (1884, 1896) and AMNH 969 used in part by Holland (1906, 1924) in reconstructions of the skull of *Diplodocus* are also tentatively accepted as belonging to this genus.

### EXTERNAL FEATURES

The shape and proportions of the skull of *Diplodocus* have been accurately reconstructed by Marsh (1884, 1896; see also Ostrom and McIntosh, 1966) and Holland (1906, 1924); in some details these aspects of Marsh's reconstructions are more exact. One apparent error in Marsh's restorations of the shape of the skull, however, should be noted. In his dorsal views of the skull the steeply pitched, lateral surface below the larger, posterior, antorbital opening is incorrectly shown as being broadly bowed laterally, rather than flat. Whereas Marsh's restorations omit some of the sutures and inaccurately show the courses of a few, Holland's not only incorrectly show the extent of many of the bones, but erroneously depict the presence of others, such as a supraorbital and postfrontal. Most of the errors in the literature that pertain to the external features of the skull of *Diplodocus* concern the sutural pattern of the posterior half of the skull; the description that follows is mainly intended to resolve this confusion. Most of this information is readily visible in Figs. 2 and 3.

In dorsal view the cranial roof is dominated by the broad, flat frontals. They contact the fused parietals posteriorly in a nearly straight, transverse suture that extends laterally to nearly the upper end of the supratemporal fossa; at this point the frontal-parietal contact continues a short distance as it turns abruptly anteriorly to skirt the upper end of the fossa. Lateral to the frontal-parietal suture the frontal is drawn outward into a transversely oriented, nearly vertical wing that extends ventrally to contact on its posterior surface a dorsal, medially expanded process of the postorbital; the plane of their contact is oriented obliquely anteroventrally in sagittal section. The anterior surface of the lateral wing of the frontal forms the posterodorsal portion of the orbital border and wall. The posterior surface of the frontal wing is extensively overlapped by the postorbital and their surface line of contact extends outward and downward along the anterodorsal margin of the supratemporal fossa so that the frontal makes little or no contribution to the fossa wall. Seen from above the frontal portion of the orbital rim is deeply concave. The nasal-frontal suture is sinuous and extends laterally, meeting the prefrontal a short distance posterior to its medialmost level of projection. The anterolateral corner of the frontal is deeply incised by the narrowly triangular, posteromedially directed, posterior half of the prefrontal. The fused parietals are narrowly exposed on the skull roof, where they taper somewhat as they extend toward the supratemporal fossa. A vertically oriented, lateral wing of the parietal, forming the posterior wall of the supratemporal fossa, has an extensive occipital exposure. The lateral wing of the parietal is triangular in cross-section and thins toward its outer edge, which in occipital view is greatly expanded dorsolaterally into a smooth, broadly convex border.

In CM 3452 the intersection of the median union of the frontals with the fused parietals is well preserved and, as Holland (1924) pointed out, a parietal opening is absent. Holland also noted the absence of such an opening in the *Diplodocus* skull CM 662, but claimed that a medial opening was present in the parietal region of the skull roof of the probable *Diplodocus* skulls CM 11161, AMNH 969, USNM 2672 and USNM 2673, and the probable *Apatosaurus* skull CM 11162. We can find no evidence that this opening existed in these specimens. Though in none of the specimens illustrated here can the presence of a midline suture of the nasals be verified, it is assumed that Marsh (1884, 1896) and Holland (1906, 1924) were correct in describing the nasals as paired. The paired nasals form the posterior margin of the narial opening; each is slightly concave

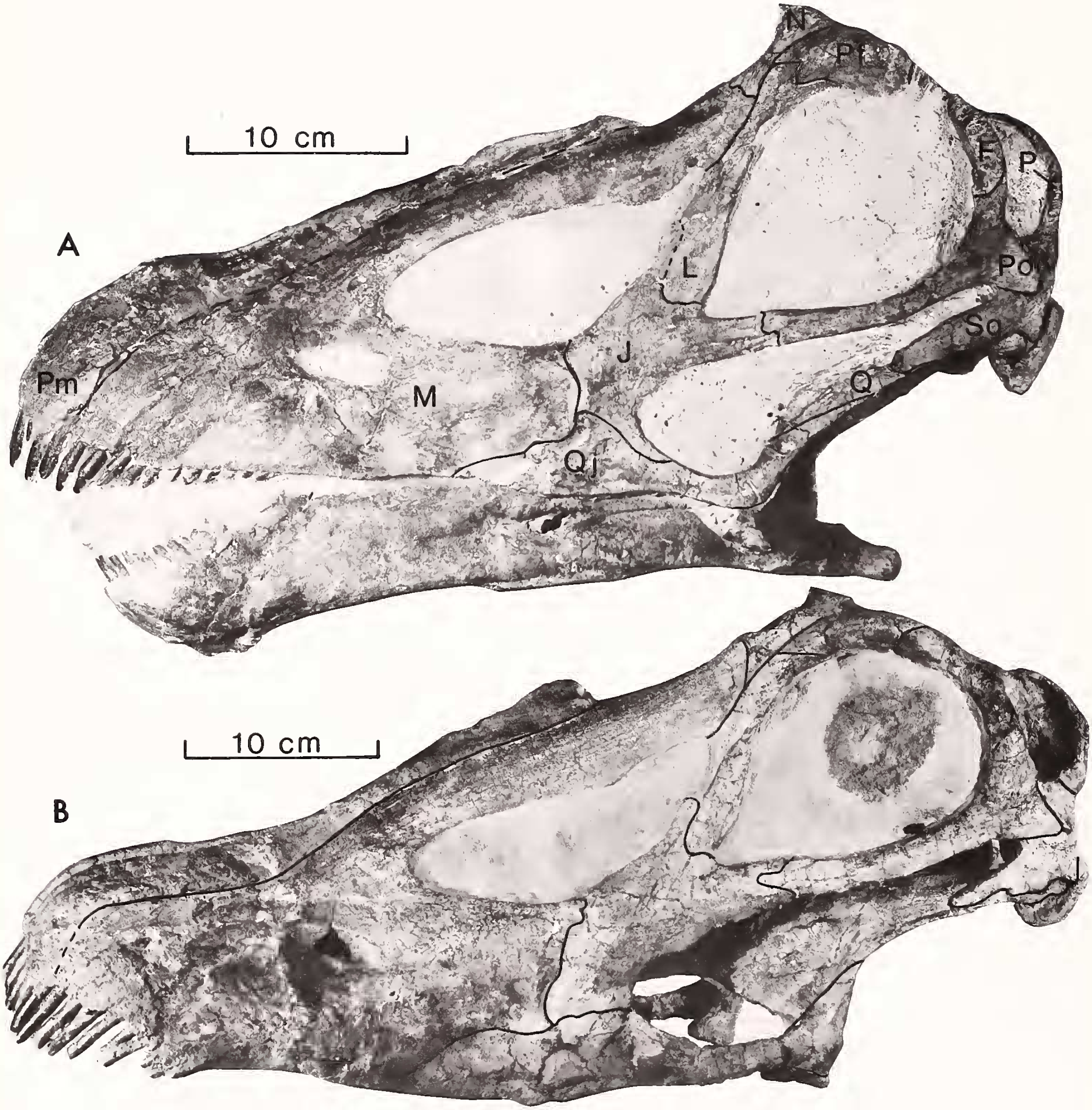

Fig. 2.—Skulls of *Diplodocus*. A, CM 3452, and B, CM 11161.

along this border, so that together they project somewhat forward into the narial opening along the midline. Laterally the nasal continues anteroventrally as a narrow, strip-like process that contacts the anterior half of the medial border of the prefrontal while bounding the posterolateral border of the narial opening. The anterior end of this process in CM 11161 is strongly beveled anteroventrally to form a short, sharply pointed lappet of bone that overlaps the upper end of the ascending process of the maxilla and contacts the anterior margin of the upper end of the lacrimal. The anteroventral pro-

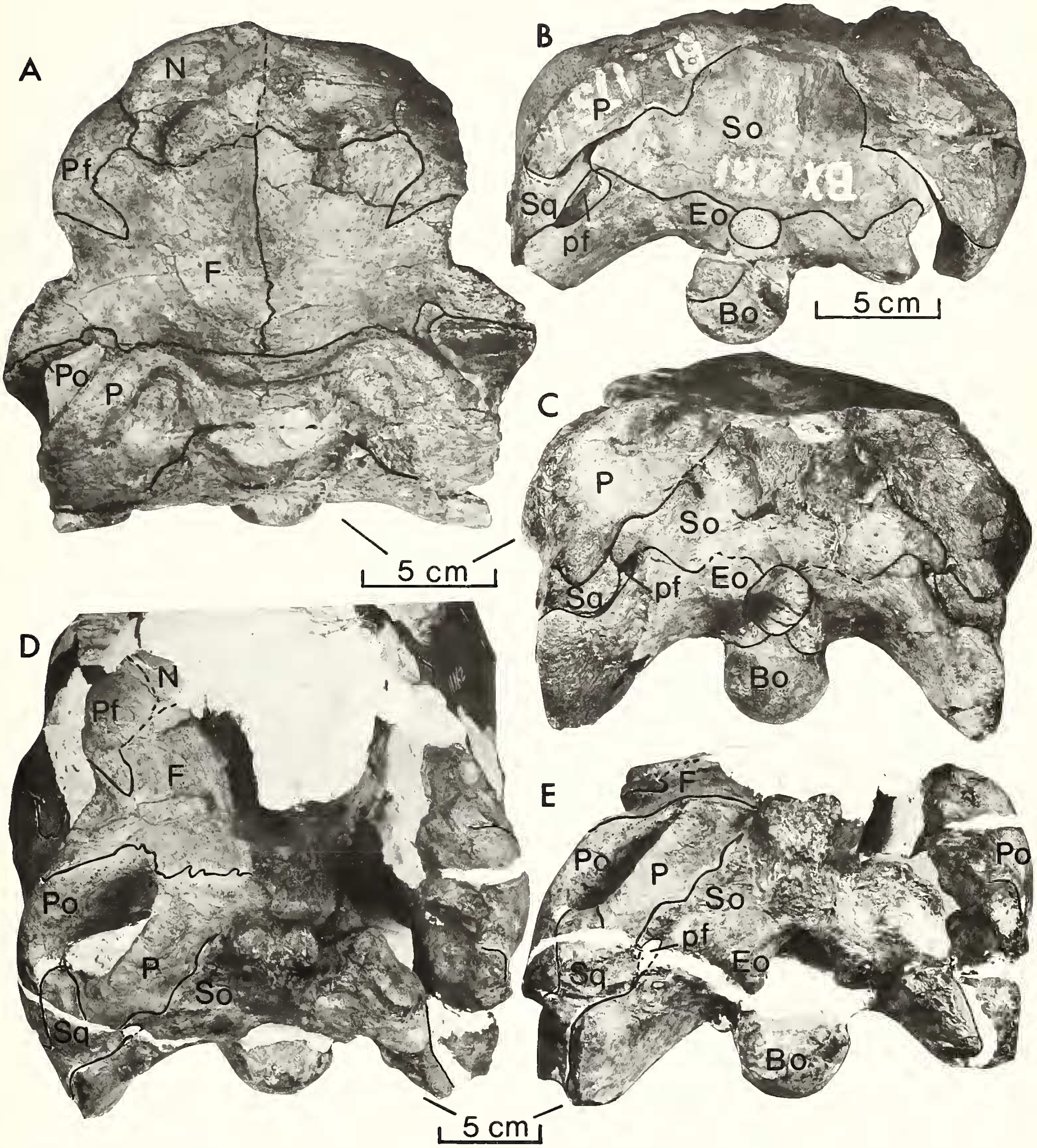

Fig. 3.—A, cranial roof, and C, occipital views of *Diplodocus* skull CM 3452. B, occipital view of *Diplodocus* braincase CM 26552. D, cranial roof, and E, occipital views of probable *Apatosaurus* skull CM 11162.

cess of the left nasal of CM 3452 appears to differ from that of CM 11161 by terminating in a border that is normal to its long axis.

The prefrontal enters the anterodorsal margin of the orbit and in lateral view its sharply pointed anterior end wedges between the nasal and lacrimal. In CM 11161 the prefrontal-lacrimal suture extends directly posteromedially across the dorsal wall of

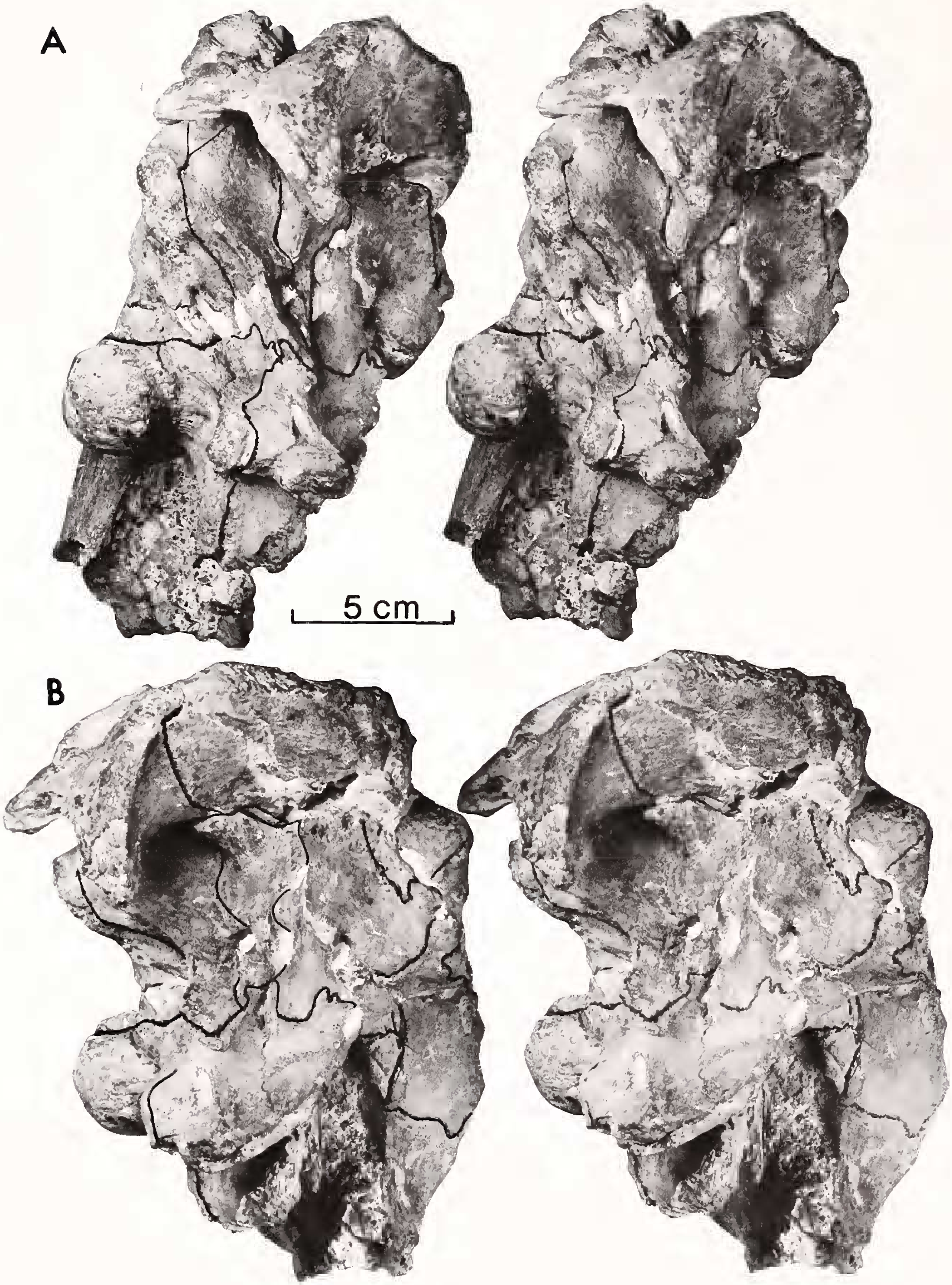

Fig. 4.—A, ventrolateral, and B, anterolateral stereo views of *Diplodocus* braincase CM 26552. Structural features indicated in Fig. 6.

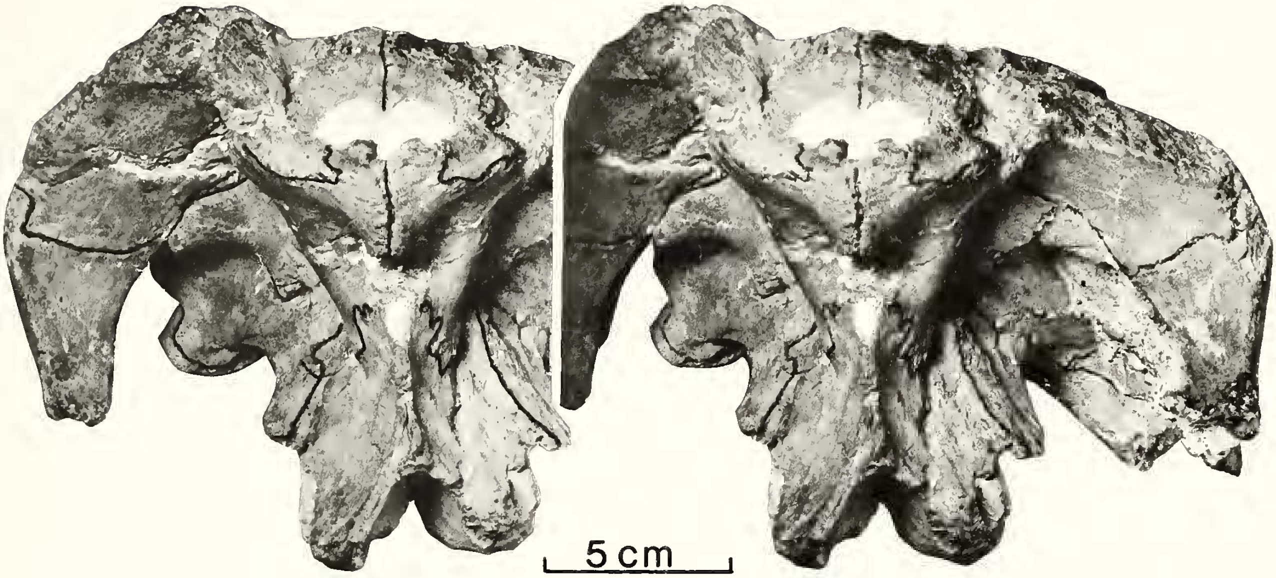

Fig. 5.—Anterior stereo view of *Diplodocus* braincase CM 26552. Structural features indicated in Fig. 6.

the orbit, whereas in CM 3452 there is a sharply angular jog in this suture. The jugal makes a small contribution to the anterior end of the ventral margin of the orbit. From the anteroventral corner of the orbit the jugal-lacrimal suture, best preserved in CM 11161, runs a short distance anteriorly, then swings abruptly dorsally, forming the posterior border of a narrow, dorsal process of the jugal, as it extends for a somewhat longer distance to reach the antorbital opening. The bluntly rounded, distal end of the dorsal process of the jugal, incomplete in the skulls CM 11161 and CM 3452 but well illustrated in the restorations by Marsh (1884, 1896; see also Ostrom and McIntosh, 1966) and Holland (1906), projects a short distance dorsally and slightly anteriorly into the posterior corner of the antorbital opening. The dorsal process of the jugal and a broadly convex expansion of the ventral margin of the ascending process of the maxilla opposite this process greatly constrict the antorbital opening. Sutural contacts of the jugal with the maxilla and quadratojugal are accurately depicted in the restorations by Marsh and Holland and are well preserved in CM 3452.

The postorbital is basically triradiate in shape. A thick, medially expanded, dorsal blade forms the anterior wall of the supratemporal fossa and contacts the parietal in a nearly vertical suture on the medial wall of the fossa. In lateral view the postorbital-frontal suture extends obliquely across the posterolateral edge of the orbit at about its mid-height, then turns sharply ventromedially across the posterior wall of the orbit (Figs. 4–6). Thus the postorbital forms the ventral half of the posterior orbital wall. A short, broadly triangular, posterior process of the postorbital overlaps the squamosal. A third, greatly attenuated, anterior process of the postorbital bounds almost the entire ventral margin of the orbit; its suture with the jugal is clearly preserved in CM 3452 and its essentially vertical orientation is in marked contrast with the nearly horizontal contact depicted in previous accounts. In CM 11161 this suture is not well defined and the anterior process of the postorbital appears to have a wedge-shaped, overlapping contact with the jugal. The squamosal can also be described as consisting of basically three processes, all emanating from the posteroventral corner of the lateral side of the skull. A narrow, dorsomedially directed, occipital process of the squamosal is described in detail below. The narrow, ventral border of the supratemporal fossa is bounded by an anterodorsal process of the squamosal that is interposed between the distal end of the lateral wing of the parietal and the superior border of the posterior process of the postorbital. A third, tongue-like process is directed anteroventrally along the lateral margin of the proximal end of the quadrate. The proximal head of the quadrate, which fits into a shallow concavity on the ventral surface of the squamosal, is narrowly exposed by

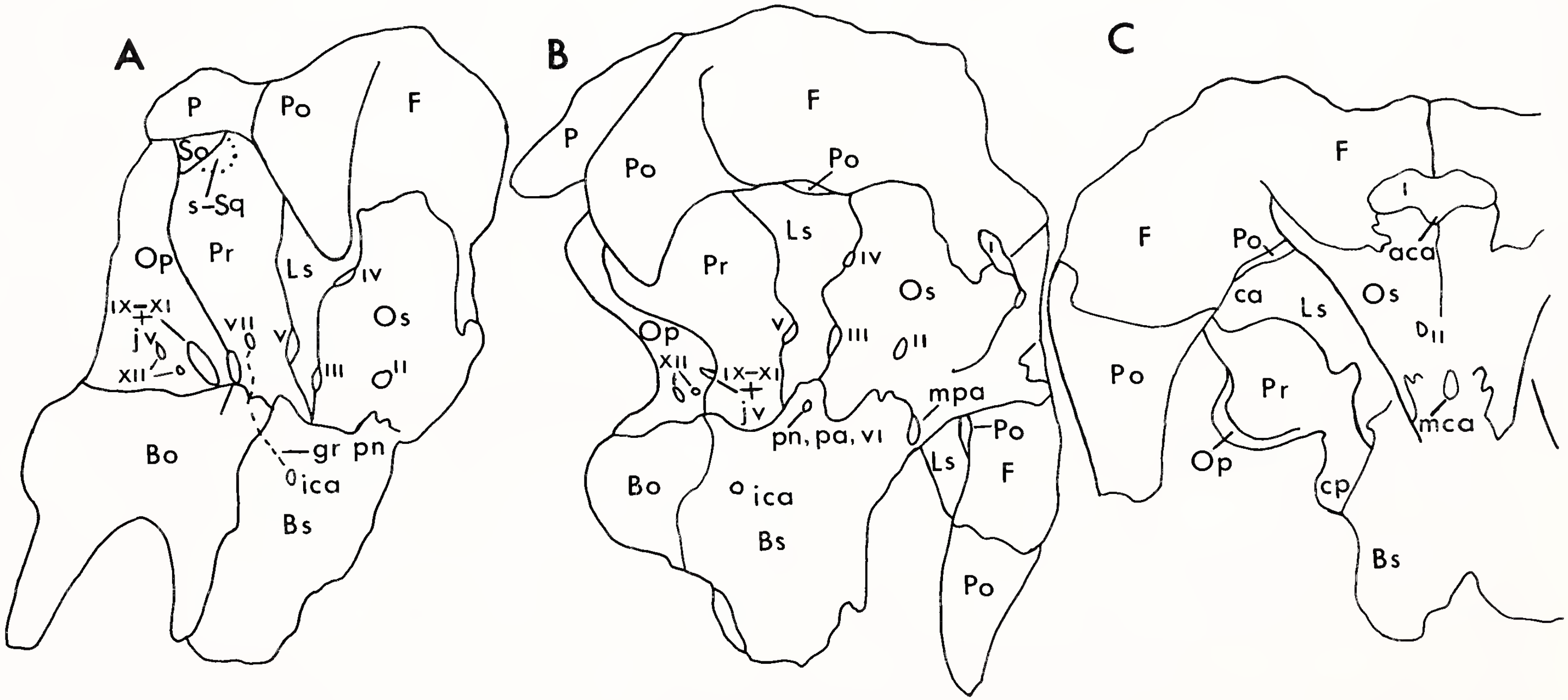

Fig. 6.—A, B, C, outline sketches of views of *Diplodocus* braincase CM 26552 of Figs. 4 and 5 with major structural features indicated.

a concave notch at the posterior end of the ventral margin of the quadrate process of the squamosal. The upper half of the anterior surface of the flared, distal end of the paroccipital process abuts against a narrow, slightly concave recess on the posteromedial edge of the squamosal below its occipital process and also buttresses the head of the quadrate; the lower half of the anterior margin of the flared end of the paroccipital process is free of contact. The posterior end of the quadratojugal has an extensive, overlapping contact with the lateral surface of the distal end of the quadrate. The ventral margin of the quadratojugal curves very slightly ventrally as it crosses the quadrate only a short distance above its distal end; the quadratojugal then turns dorsally for a considerable length, where it terminates by smoothly tapering toward the posterior margin of the quadrate. Although the quadratojugal and the squamosal closely approach each other along the lateral margin of the quadrate, they do not meet.

### Braincase

The first detailed description of the braincase of *Diplodocus* was given by Holland (1906) and was based on a well-preserved posterior portion of skull, CM 662 (now at Houston Museum of Natural Science). A critique of this paper was published by Hay (1908), who challenged many of Holland's determinations of the bones and foramina. In particular, he pointed out that the supraoccipital occupies a much larger area than that assigned to it by Holland, and that Holland's failure to recognize the presence of the proötic was the basis of many of his errors. Both interpretations, however, contain a great number of significant errors. Osborn (1912) presented an illustration of the braincase of AMNH 694 in sagittal section, which accurately depicts the internal positions of most of the cranial foramina. However, in this figure and in one other, showing the same specimen in frontal view, he not only omitted the sutures of almost all of the bones, but also incorrectly indicated the extent of others. Von Huene (1914) gave a rough sketch of the lateral aspect of the braincase of the same specimen used in Holland's (1906) study. Though most of the foramina are indicated and correctly identified, his essentially diagrammatic illustration does not show some of the cranial sutures. In Marsh's restorations of the skull of *Diplodocus* (1884, 1896; see also Ostrom and McIntosh, 1966) no attempt was made to denote the bones of the occiput. Finally, in a reconstruction by Marsh of the skull in midsagittal section, published for the first time by us (McIntosh and Berman, 1975), the braincase is depicted in only a general way. Figs. 3–6 may largely take the place of a detailed description of the braincase.

The occiput (Fig. 3), whose shape and general features are best preserved in CM 3452, is of typical sauropod form. The occiput is subrectangular in outline and is formed by the basioccipital, exoccipitals, supraoccipital, fused parietals, and a small process of the squamosal. In none of the specimens (CM 26552, CM 11161, and CM 3452) has it been possible to trace the suture between the exoccipital and the opisthotic; thus these two elements became completely fused early. It is assumed, however, that a large but undetermined portion of this compound element exposed on the occiput and the part which encloses the two openings for cranial nerve XII at the extreme posteroventral corner of the lateral wall of the braincase represent the greater part of the surface extent of the original exoccipital. The original opisthotic, bounded by the exoccipital posteriorly and the proötic anteriorly, undoubtedly included the narrow span between the foramen for cranial nerves IX–XI and the fenestra ovalis and then presumably extended dorsolaterally as a flattened process that covered the anterior surface of the exoccipital in the paroccipital process. The exoccipital bounds the lateral wall of the foramen magnum, is separated from its mate in the roof of the foramen magnum by the supraoccipital and in the floor by the basioccipital, and makes a small contribution to the dorsolateral surface of the occipital condyle and its articular surface. Only in CM 26552 is the supraoccipital-exoccipital suture clearly preserved. The exoccipital extends directly outward from the foramen magnum, making contact with the supraoccipital above in a broadly undulating suture that laterally reaches the dorsal margin of the small posttemporal fossa. At the level of the upper end of the posttemporal fossa the exoccipital-oposthotic complex bends downward to form a broad paroccipital process, constricting in breadth somewhat as it bounds the medial side of the posttemporal fossa, then expanding again distally where it contacts the squamosal and quadrate. A hook-like process at the ventrolateral corner of the supraoccipital forms the dorsolateral margin of the posttemporal fossa. The remainder of the lateral border of the fossa is completed by a narrow, occipital process of the squamosal. It enters the occiput by extending medially between the ventrolateral corner of the lateral, occipital wing of the parietal and the dorsal margin of the expanded end of the paroccipital process, then turns upward along the ventromedial side of the parietal to meet the hook-like process of the supraoccipital. From this point the occipital process of the squamosal continues a very short distance, still in contact with the parietal but in front of the hook-like process of the supraoccipital; the end of the occipital process of the squamosal contacts a small area on the superior edge of the anterolateral face of the proötic (Fig. 3).

In ventrolateral view the exoccipital pedicle is triangular, widening toward its ventral contact with the basioccipital where it encloses three foramina and bounds the posterior wall of a fourth. The most posterior of these openings is oval and carried the posterior branch of cranial nerve XII. Immediately anterior to this is a very small, round opening presumably for an anterior branch of the same nerve. The largest and most anterior foramen enclosed by the opisthotic is elongate (about 17 mm high and about 4 mm wide), is inclined posterodorsally, and faces somewhat posteroventrally; often referred to as the jugular foramen, it presumably transmitted nerves IX–XI and probably the jugular vein. Anterior to the jugular foramen the narrow fenestra ovalis opens on the boundary between the opisthotic and proötic. The proötic, an extensive element, is surrounded by the opisthotic and supraoccipital behind, the basioccipital and basisphenoid below, the laterosphenoid in front, and the parietal above. The proötic is tightly sutured to all of these elements except the laterosphenoid and parietal, with which it has abutment contacts. Exposed mainly as a broad, flat plate that faces anterolaterally, the proötic extends only slightly onto the anterior surface of the proximal end of the paroccipital process. Below the level of its contribution to the paroccipital process the proötic is deeply exposed posteriorly, forming a narrow, laterally projecting lamina of bone that extends downward to the ventralmost point of contact of this bone with the basisphenoid. The lateral edge of the lamina is deeply emarginated into a smooth, broad, concave arc; the lamina forms the body of the crista proötica. The lower portion of the proötic encloses one foramen and impinges on two others. Posteriorly it forms the anterior border of the fenestra ovalis. From the dorsal border of this opening two shallow, parallel grooves of nearly equal dimensions, one on either side of the proötic-opisthotic suture, extend posterolaterally to about where the suture between them turns abruptly upward across the anterior face of the proximal end of the paroccipital process. Directly anterior to the fenestra ovalis the posterior face of the crista proötica is perforated by a small round foramen for the VII nerve. A large, subcircular exit for nerve V, measuring about 8 mm in diameter, is positioned on the boundary between the proötic and laterosphenoid and at the same level as the facial nerve opening.

The laterosphenoid is a narrow, wing-like structure that is principally exposed as a flat, anterolaterally facing surface. It is strongly sutured to the basisphenoid below, but has an abutment contact with the proötic behind, the orbitosphenoid in front and the postorbital above. A short distance above its narrow contact with the basisphenoid the laterosphenoid forms the anterior margin of the trigeminal foramen and the posterior margin of the oculomotor foramen; the latter foramen is about 11 mm high and about 4 mm wide. A smooth, concave notch in the laterosphenoid margin of the trigeminal foramen probably allowed the forward passage of the ophthalmic branch of nerve V. Extending downward from the ventral border of the trigeminal foramen along the lateropehnsoid-orbitosphenoid contact is a deep channel that probably carried the maxillary and mandibular branches of this nerve. An ovate foramen for the trochlear nerve, measuring approximately 7 mm high and 4 mm wide, opens on the laterosphenoid-orbitosphenoid suture dorsal to the oculomotor foramen. As the laterosphenoid extends above the level of the trigeminal foramen it expands outward to form a thick, laterally arching lamina of bone, the crista antotica. The convex dorsal edge of the crista antotica fits into a shallow, concave channel on the ventromedial edge of that part of the postorbital forming the anterior wall of the supratemporal fossa. In anterior view of the braincase the lateral wing of the frontal, which forms the posterodorsal wall of the orbit, nearly hides from view the laterosphenoid-postorbital contact. The lateral wing of the frontal tapers to a thin edge toward the ventromedial margin of the posterodorsal wall of the orbit and does not make substantial contact with the laterosphenoid. The orbitosphenoid, which forms the anteriormost component of the lateral wall of the braincase, may possibly include some portion of the presphenoid. Its posterior portion, which forms the anterior margins of the openings for nerves III and IV, is in the form of a stout vertical pillar whose expanded ends have a digitating suture with the frontal above and the fused basisphenoid-parasphenoid below. A short, thick process projects posteriorly from about mid-length along its posterior margin to separate the oculomotor and trochlear foramina. Immediately anterior to the oculomotor foramen and close to the midsagittal plane is a large, anterolaterally directed opening for the optic nerve, measuring about 8 mm high and 5 mm wide. At the level of the optic foramen the orbitosphenoid extends forward a short distance as it converges on the midline to unite with its mate. Dorsally the united orbitosphenoids form the ventral borders of the very large, nearly coalesced canals for the olfactory tracts, whereas ventrally they extend in front of and a short distance below the optic foramina to contact the basiparasphenoid complex; the portion of the paired orbitosphenoids forming the anteromedial borders of the optic foramina is nearly missing in CM 26552, but is well preserved in CM 11161 (not shown here). Small, blunt processes on the orbitosphenoid margins of the olfactory canals, one on either side of the midline suture, form a small cleft through which probably passed the anterior cerebral artery, a branch of the internal carotid artery. A short distance anterior to the orbitosphenoid in CM 11161 are fragments of a thin vertical plate of bone (not shown here) oriented on the midsagittal plane of the skull, which may represent remnants of the presphenoid portion of the interorbital septum.

The basioccipital appears to form the greater part of the articular surface of the condyle. The condyle is convex posteriorly and ventrally, and flattened dorsally. The long axis of the condyle is oriented at about a right angle to a plane passing through the jaw margins, indicating that the head was tilted at about a right angle to the neck. Between the condyle and the basal tubercles the inferior face of the basioccipital arches anterodorsally, then curves smoothly downward and slightly backward to form the caudal halves of the basal tubercles. The tubercles diverge slightly ventrolaterally and their posterior surfaces are separated by a deep furrow. Forming the cranial floor anterior to the basioccipital is the basisphenoid; it is completely fused with the parasphenoid, which is principally represented by the parasphenoidal rostrum. The parasphenoidal rostrum is broken off at its base in CM 26552 but is well exhibited in CM 11161 (Fig. 8). The basisphenoid forms the anterior halves of the basal tubercles, the long, slender, anterolaterally directed basipterygoid processes (broken off at their bases in CM 26552) and the inferior margin of the crista proötica. There is a deep, smooth spheroidal depression between the bases of the basipterygoid processes; this depression is bounded anterolaterally by a narrow, ridge-like projection along the anteroventral surface of the proximal third of the basipterygoid process which merges with the ventral edge of the narrow, blade-like parasphenoidal rostrum. Above the basipterygoid processes the lateral walls of the basisphenoid converge anteromedially to become smoothly continuous with the rostrum. The entrance for the internal carotid artery and the palatine branch of the facial nerve into the basicranium, via the vidian canal, is in its normal location on the ventrolateral surface of the basisphenoid between the inferior border of the crista proötica and the base of the pterygoid process. The vidian canal begins at the upper end of an approximately 5-mm-wide groove that extends a short distance anteroventrally onto the base of the basipterygoid process. A faint groove, extending ventrally from the lower rim of the facial foramen to a smooth notch in the dorsal edge of the vidian canal (Fig. 4), presumably traces the course of the palatine branch of the facial nerve. Directly below the foramina for cranial nerves III and V is a small, round opening for the exit of the palatine branch of the carotid artery, the palatine branch of the facial nerve and probably the abducens nerve. On the midline of the basiparasphenoid complex and immediately above the dorsal edge of the adjoining rostrum is a narrow, vertical opening that probably transmitted the paired, median palatine branches of the carotid arteries.

## PROBABLE SKULL OF *APATOSAURUS*

### DESCRIPTION OF SKULL CM 11162

The large skull CM 11162 that was closely associated with the postcranial skeletons of *Apatosaurus louisae* field no. 1 (type, CM 3018) and *Apatosaurus* field no. 40 at Carnegie quarry (Fig. 1) and presumed to belong to one of these specimens, conforms closely to the skull of *Diplodocus*, despite some postmortem distortion. The skull is missing the lower jaw and has been variably crushed dorsoventrally (Fig. 7); though the right side of the

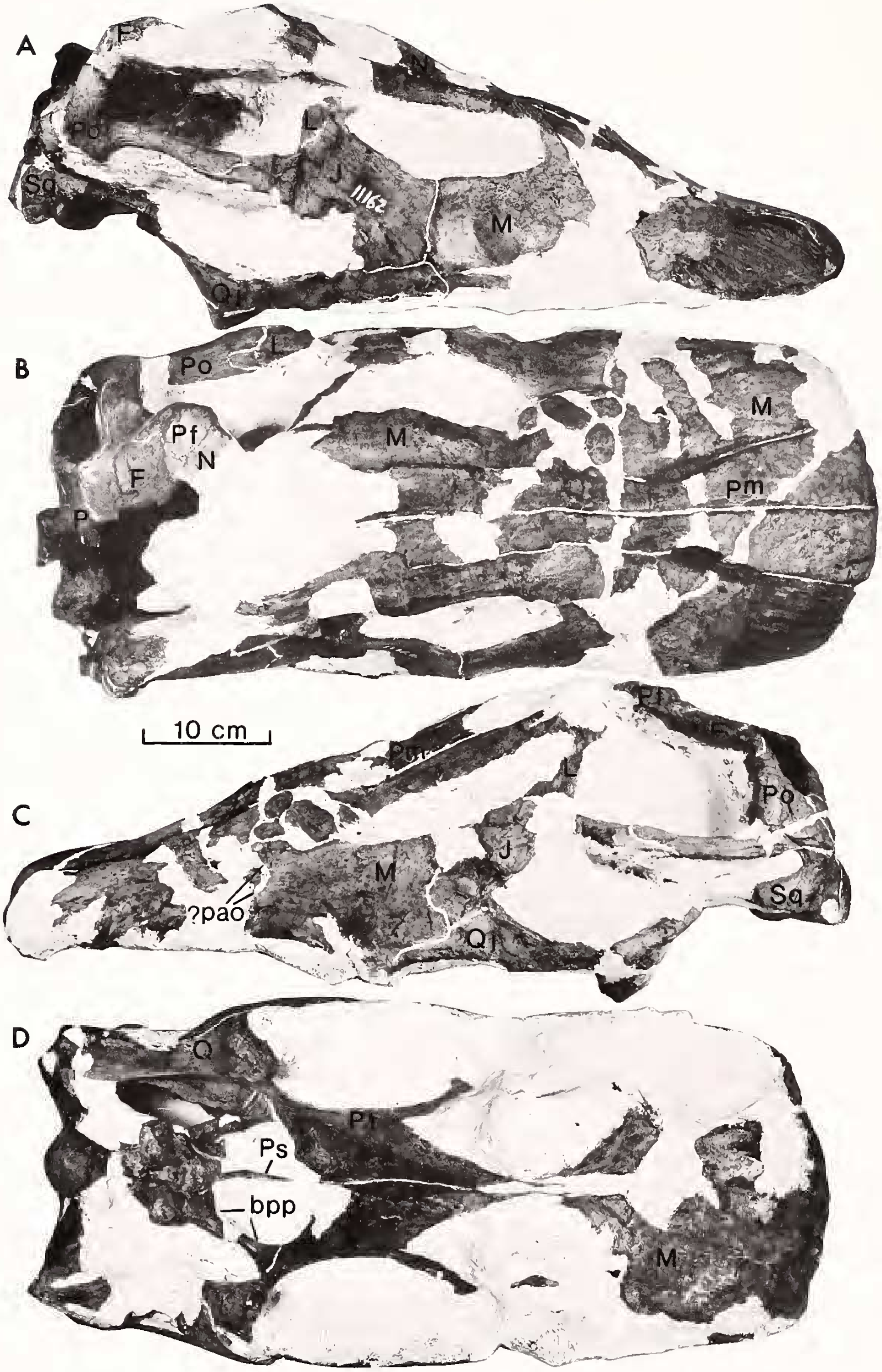

Fig. 7.—A, right lateral, B, dorsal, C, left lateral, and D, ventral views of probable *Apatosaurus* skull CM 11162.

skull has retained, for the most part, its proper pitch, the left side has undergone flattening, giving it a broader appearance, especially in the snout region. Distortion and incomplete preservation make impossible determination of the exact outlines of all the major skull openings except for the left supratemporal fossa. However, there is no structural evidence that they differed in any important way from those in *Diplodocus*; this is certainly true of the supratemporal fossa. Skull dimensions of CM 11162 are given in Table 1. In lateral view the angles subtended between the meeting of the projections of the occipital plane with a plane passing through the ventral margins of the maxillae, the occipital plane with the cranial roof, and the cranial roof with the dorsal margin of the snout are about 75, 120, and 140 degrees, respectively. A restoration of CM 11162 in lateral view is given in Fig. 8.

Table 1.—*Measurements (in mm) of skulls assigned here to* Diplodocus *and* Apatosaurus. *1, skull length, measured from snout tip to posterior margin of occipital condyle; 2, skull width, measured at ventralmost level of quadrates; 3, greatest length of quadrate, measured through shaft; 4, skull length to quadrate length ratio; 5, length to distal width ratio of quadrate.*

| Taxa and catalog numbers | Measurements | | | | |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 |
| *Diplodocus* | | | | | |
| CM 11161 | 515 | 178 | 185 | .36 | .20 |
| CM 3452 | 440 | — | 167 | .38 | .19 |
| USNM 2672 | 550 | 190 | 183 | .33 | .22 |
| USNM 2673 | 600 | — | 215 | .36 | .22 |
| *Apatosaurus* | | | | | |
| CM 11162 | 650 | 280 | 185 | .28 | .30 |

The incompletely preserved external dermal bones of CM 11162 do not differ greatly from those of *Diplodocus*. The premaxillae are well preserved and show that each possessed four or five functional teeth, represented by their bases. The maxillae are fairly well represented except for two important structures. The upper ends of their ascending processes have been lost, so their sutural relationships with the nasals and lacrimals are indeterminate. Also, it is not certain if the smaller, more anterior of the two antorbital openings of the maxilla that is characteristic of *Diplodocus* is present. The posterior rim of the preantorbital opening of the left maxilla is hesitantly identified in Fig. 7C; its position would approximate that in *Diplodocus*. A small, isolated fragment of bone lies in what would be the position of this opening. A tooth count is possible for only the right maxilla, where it is based on replacement teeth, or in most instances their impressions, which have been exposed by the loss of surface bone of the maxilla; the right maxilla may have held as many as 12 or 13 functional teeth. The teeth of CM 11162 are identical to the very slender, cylindrical teeth of *Diplodocus*. The jugal and quadratojugal, best preserved on the right side of the skull, show their boundaries with each other and the maxilla. The distal end of the dorsal process of the right jugal projects into the antorbital opening as in *Diplodocus*. Remnants of the lacrimals remain. The contacts of the left postorbital are clear except for that with the parietal, which in *Diplodocus* extends vertically down the innermost level of the supratemporal fossa wall. The right squamosal is fragmentary; the left is nearly complete except for the loss of the distal end of its anteroventrally directed quadrate process and has suffered little distortion, exhibiting the same basic relationships with is bordering elements as in *Diplodocus*.

All that remains of the cranial roof (Fig. 3D) is the greater part of the left side. The left parietal is nearly complete, missing only a small portion of its medial boundary; the other sutural boundaries of the left parietal are distinct except for the dorsomedial end of its contact with the supraoccipital on the occiput and its contact with the postorbital. Approximately a fourth of the left frontal is lost along its medial border. The preserved portion of its posterior suture with the parietal and postorbital is distinct and rather dentate for about the medial half of its length; the orbital margin of the frontal exhibits the same concave emargination seen in *Diplodocus*. Also as in *Diplodocus*, the triangular, posterior half of the prefrontal penetrates deeply posteromedially into the anterolateral corner of the frontal. The posterior two thirds of the prefrontal projection into the frontal is well defined, but its anteromedial contact with the frontal and nasal is hesitantly traced. The anterior portion of the prefrontal is absent. Only a short, narrow strip of the nasal is preserved along the medial border of the prefrontal; its contact with the frontal is not clear.

The somewhat abraded occiput (Fig. 3E) is nearly intact on the left side, whereas the greater part of the right side is absent. Only the supraoccipital-exoccipital suture of the occiput cannot be found. The median, nuchal crest on the supraoccipital above the foramen magnum is strongly developed. The small, left posttemporal fossa is clearly visible and is identical to that of *Diplodocus* in outline and in the way its borders are formed. The articular surface of the occipital condyle is hemispherical except

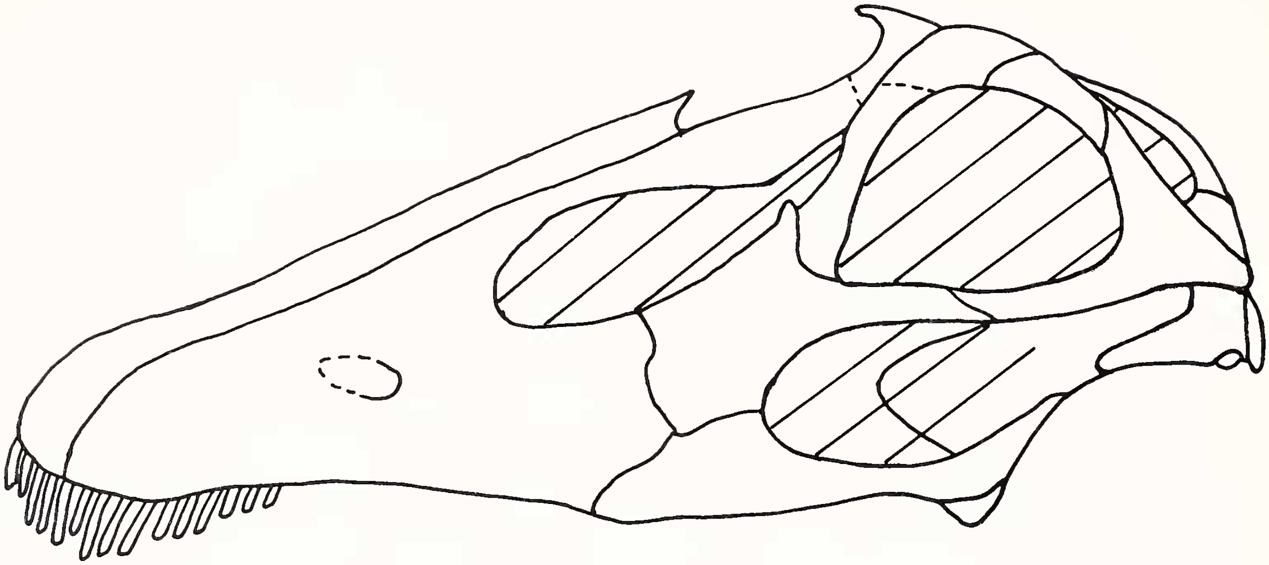

Fig. 8.— Restoration of probable *Apatosaurus* skull CM 11162.

for its flat, even possibly slightly concave, dorsal margin. The axis of the condyle is directed posteroventrally at about 120 degrees from the long axis of the skull; this angle may have been exaggerated by dorsoventral crushing. A widely open fracture that extends across the floor of the foramen magnum, giving this otherwise round opening a vertically elongate appearance, continues outward and slightly upward through the posterior process of the postorbital on the lateral side of the skull. The basicranium (Fig. 7D) contains a number of major and minor fractures along some of which there has been displacement. Except for proportional differences discussed below, the basicranium of CM 11162 exhibits no marked structural differences from that of *Diplodocus*.

With the exception of proportional differences, the partially preserved palate of CM 11162 (Fig. 7D) exhibits no noticeable departures from that described (McIntosh and Berman, 1975) for *Diplodocus*. The pterygoids are essentially complete, undistorted and, as in *Diplodocus*, form a midventral, dihedral angle between them of about 60 degrees. The palatines, which presumably would have occupied the acute angle formed between the narrow, transverse process and the anterior process of the pterygoids, are absent. Both vomers are lost, but they undoubtedly occupied the same position as those in *Diplodocus* (McIntosh and Berman, 1975); there the flat, narrowly triangular vomers articulate with the lateral surface of the broadly concave, anteroventral portion of the pterygoid borders for most of their length and their anterior ends are clasped together at the midline by broad, medially directed processes of the maxillae. The maxillary processes are well preserved in CM 11162 and the medial gap between them, which held the anterior ends of the vomers, is somewhat wider than normal due to the dorsoventral flattening of the snout. Both ectopterygoids appear to be absent, although they may be buried in the remaining matrix. The right quadrate is essentially complete, undistorted and in its proper orientation, whereas the left is badly crushed and missing a large central section.

## Comparison of CM 11162 with *Diplodocus*

Though the incomplete preservation of the skull CM 11162 eliminates many opportunities for detailed comparisons, this skull is obviously very close to that of *Diplodocus*. Comparisons between CM 11162 and *Diplodocus* skull CM 3452 and those skulls very likely belonging to *Diplodocus* have revealed a number of subtle proportional and structural differences. Some of these differences, however, have to be evaluated with caution because they may be the result of postmortem distortion of CM 11162. It will also be noticed that the obviously greater general robustness of CM 11162 is a fundamental aspect of many of the features used below to contrast it with the skull of *Diplodocus*.

In lateral view the occiput of the probable *Apatosaurus* skull CM 11162 slopes anterodorsally at an angle of about 75 degrees to the horizontal passing through the ventral margins of the maxillae as compared to its right angle orientation in *Diplodocus* (Fig. 2); differences they exhibit in the angles subtended between the occipital plane and the cranial roof, and the cranial roof and the snout are too small to be safely considered as diagnostic. In CM 11162 the axis of the occipital condyle is inclined posteroventrally at an angle of about 120 degrees to the long axis of the skull in contrast to its approximately right angle orientation in *Diplodocus;* the larger angle of the former, however, may be partly due to crushing. The triangular, posterior process of the postorbital of CM 11162 differs from that of *Diplodocus* in being more broadly developed and in extending to a level posterior to the supratemporal fossa. In the probable *Apatosaurus* skull there is also a greater vertical development of the squamosal below the posterior process of the postorbital, which has resulted in a corresponding lengthening of its posterior contact with the distal end of the paroccipital process; the quadrate process of the squamosal is also proportionally broader in CM 11162 than in *Diplodocus*.

Differences are also seen in the occipital views of the skulls (Fig. 3). In this aspect CM 11162 appears rather dome-shaped in outline, whereas the skull of *Diplodocus* CM 3452 is subrectangular in outline; this difference can be attributed mainly to development of the lateral, occipital wing of the parietal. In *Diplodocus* its free, superior border arches smoothly and rather strongly dorsolaterally, completely hiding the supratemporal fossa from occipital view. The lateral wing of the parietal in CM 11162 is much narrower and its nearly straight, ventrolaterally sloping, free border allows the supratemporal fossa to be partially seen in occipital view. Further, in CM 11162 the distal end of the parietal wing does not encroach as greatly upon the squamosal as in *Diplodocus* and, as a result, in the former the dorsolateral process of the squamosal, which forms the ventral border of the supratemporal fossa, is wider and the contact between the occipital process of the squamosal and the occipital wing of the parietal is considerably shorter. In *Diplodocus* the lateral surface of the skull below the supratemporal fossa meets the occiput in a sharp, right angle corner, whereas in CM 11162 this intersection is somewhat rounded. As a consequence, the probable *Apatosaurus* skull can also be distinguished from that of *Diplodocus* by its greater exposure of the squamosal and its partial exposure of the posterior process of the postorbital in occipital view. In *Diplodocus* all that can be seen of the squamosal in this view is its narrow, occipital process. In addition to this process in CM 11162, the anterodorsal process of the squamosal and a wide margin along its posterior contact with the flared, distal end of the paroccipital process are also clearly visible in occipital view.

The most marked proportional differences between CM 11162 and the skull of *Diplodocus* CM 11161 are in the palate, quadrate, and braincase (Fig. 9). Though proportionally the lengths of their braincases, measured from the back of the condyle to either the base or the tip of the paraphenoid rostrum, are very similar, the basipterygoid process of CM 11162 is shorter and stouter, and the condyle is much more massive. In CM 11162 there is a marked flaring of the distal end of the basipterygoid process, whereas in CM 11161 there is only a slight swelling. In these features of the braincase the *Diplodocus* skulls CM 3452 and CM 11161 are identical. The quadrate of CM 11162 is proportionally shorter and more massive at its distal end than in CM 11161, CM 3452, USNM 2672, and USNM 2673 (Table 1). A proportionally shorter quadrate in CM 11162 is reflected in a more posterior position of its contact with the quadratojugal than in CM 11161. Although the lengths of these contacts along the posterior borders of the quadrates of both specimens are proportionally very similar, if not equal, the posterior margin of the quadratojugal in CM 11162 is at a level slightly anterior to the median union of the basipterygoid processes, whereas in CM 11161 it is considerably posterior to this level. In this feature the *Diplodocus* skull CM 3452 is identical to CM 11161. In palatal view the angle formed between the basipterygoid processes in CM 11162 is about 60 degrees, whereas it is about 40 degrees in CM 11161. As a result, the end of the basipterygoid process in CM 11162 is brought closer through a horizontal plane to the distal end of the quadrate. The basipterygoid process and the quadrate are also brought closer together in CM 11162 because the medial surface at the distal end of its quadrate does not curve slightly laterally as in CM 11161. In CM 3452 the angle between the basipterygoid processes is about 35 degrees and the medial

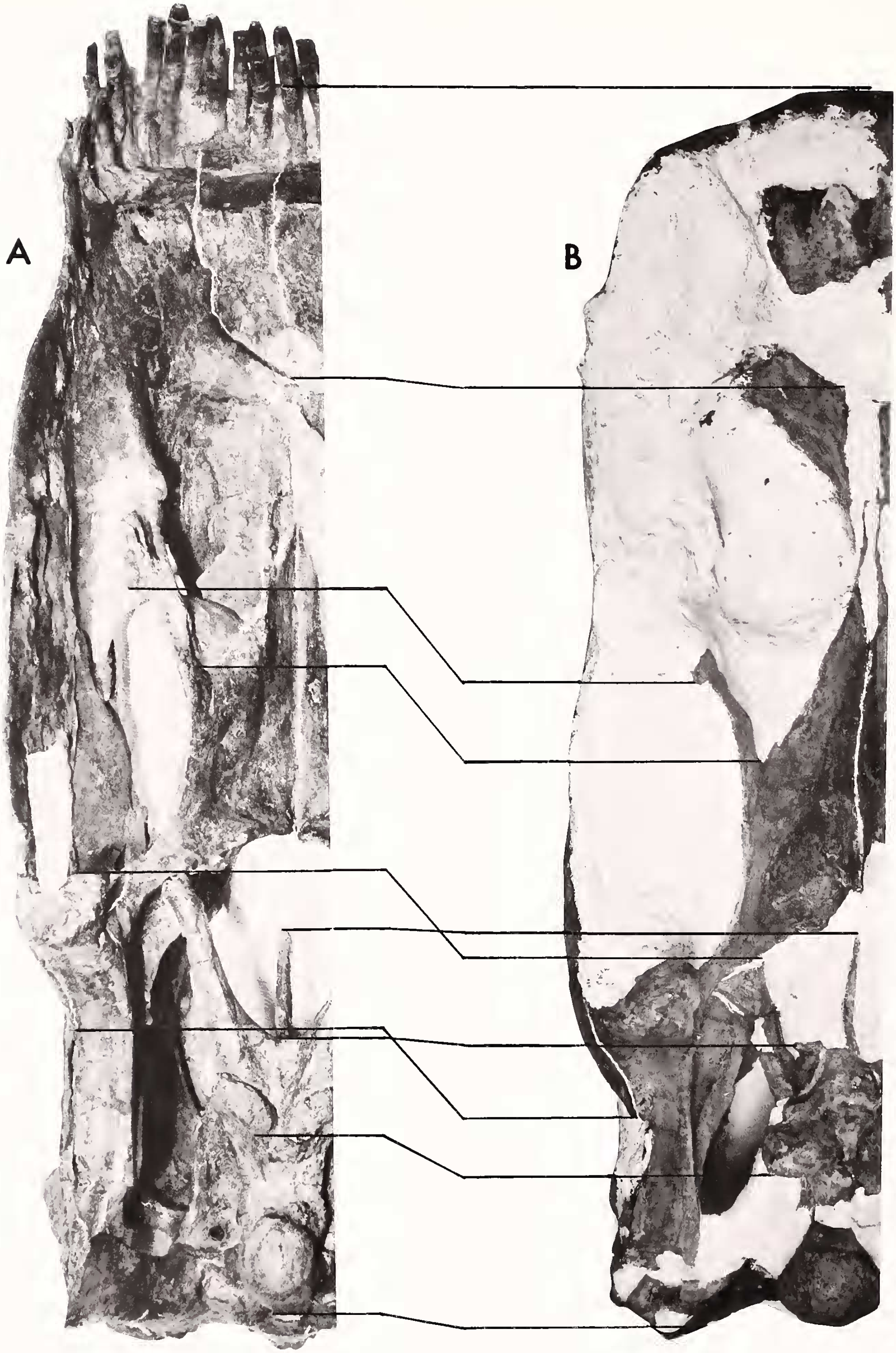

Fig. 9.—Palatal views of skulls of A, *Diplodocus* CM 11161, and B, probable *Apatosaurus* CM 11162 reduced to same size in order to demonstrate proportional differences. Horizontal lines connect identical topographical points.

surface of the quadrate also curves slightly laterally at its distal end. As a result of the proportionally shorter postpterygoid structures in CM 11162, its pterygoid occupies the more posterior position in the skull than that in CM 11161. At the level occupied by the vomers there is a disproportionate, longitudinal lengthening of the palate in CM 11162 over that of CM 11161 to the extent that, anterior to this level none of their palatal structures shows any appreciable differences in anteroposterior position.

Holland (1915*a*) stated that maxillary teeth of CM 11162 did not insert vertical to the jaw line as in *Diplodocus*, but were more or less procumbent; we cannot find any evidence to support this observation. Further, our earlier observation (McIntosh and Berman, 1975) that the probable *Apatosaurus* skull CM 11162 may differ from *Diplodocus* in the reduced size and more anterior position of the foremost antorbital opening also cannot be verified with further preparation.

## ADDITIONAL EVIDENCE ON THE SKULL OF *APATOSAURUS*

A pair of quadrates and the greater part of a cranium were found by Marsh's collectors at Morrison, Colorado, which provide additional evidence, though circumstantial, that the skull of *Apatosaurus* was *Diplodocus*-like in structure. The catalogue number YPM 1860, which both quadrates bear, is very likely their correct assignment. In reviewing the ambiguities surrounding the locality data of the cranium, it was concluded that there is not only strong reason to believe that it came from YPM quarry 10, but that it also belongs to the type of *A. ajax*, YPM 1860. Both the quadrates and the cranium represent a skull larger than any skull heretofore identified as *Diplodocus* and are also slightly larger than the presumed *Apatosaurus* skull CM 11162.

The left quadrate from Morrison (Fig. 10) is complete except for the thin, anteriorly directed plate of bone on whose medial surface the pterygoid articulated, the right quadrate is missing not only the pterygoid process, but also a little over 20% of the upper, proximal end of its main shaft. The quadrates are not only near duplicates of those of *Diplodocus* and the probable *Apatosaurus* skull CM 11162, but are readily distinguishable from those of *Camarasaurus*. White's (1958) detailed description and illustration of the quadrate of *Camarasaurus*, as well as the excellent illustrations of this bone given by Ostrom and McIntosh (1966, Pl. 4), make a close comparison here between the quadrate of this genus and the quadrates YPM 1860 unnecessary. Viewed laterally the posterior margin of the quadrate shaft curves smoothly and gently anteroventrally and has a greatest length of about 21 cm. In anteroposterior length the distal end of the shaft, measuring 3.8 cm, does not greatly exceed the proximal end, which measures 2.8 cm. The lower half of the shaft is expanded into a strongly ridged, articular surface for the posterior end of the quadratojugal; the upper, narrowly tapering end of this sutural scar extends slightly onto the posterior surface of the shaft. That part of the quadratojugal, which articulated with the quadrate, was undoubtedly like that in *Diplodocus* and the probable *Apatosaurus* skull CM 11162 in its shape and sutural relationship with the quadrate. Beginning at the anterodorsal margin of the shaft, a deep channel extends a considerable distance ventrally as it curves gradually onto and across the lateral surface of the shaft; the channel certainly held the same narrow, quadrate process of the squamosal seen in skulls of *Diplodocus* and in CM 11162. Further, the course of the channel indicates that a small portion of the lateral surface of the proximal end of the quadrate was exposed at the posterior end of the ventral margin of the quadrate process of the squamosal as in *Diplodocus*. In posterior view, the quadrate appears club-shaped. From the greatest width of about 4.8 cm near its distal, lower end, it gradually narrows dorsally to about 1.5 cm at a point approximately three fourths its height, then widens slightly to about 2.0 cm. The lower, wider portion of the posterior surface is very slightly concave except along the distal margin of the shaft, where it is moderately convex; above this region the posterior surface becomes flat and remains so until near the proximal end of the shaft, becoming here a pronounced ridge. For most of its length the medial surface of the shaft consists of a strongly developed ridge; dorsally the ridge merges with the nearly flat, narrow, proximal end of the shaft. Only the base of the anteriorly projecting pterygoid process is preserved, but the general outline and orientation of the process can be largely deduced from its remaining margins. Anterior view of the quadrate reveals the base of the pterygoid process as a rather thin plate that is broadly bowed laterally. The base of the process is thinnest at mid-height, thickening only somewhat dorsally, but greatly thickening ventrally. Below the pterygoid process the

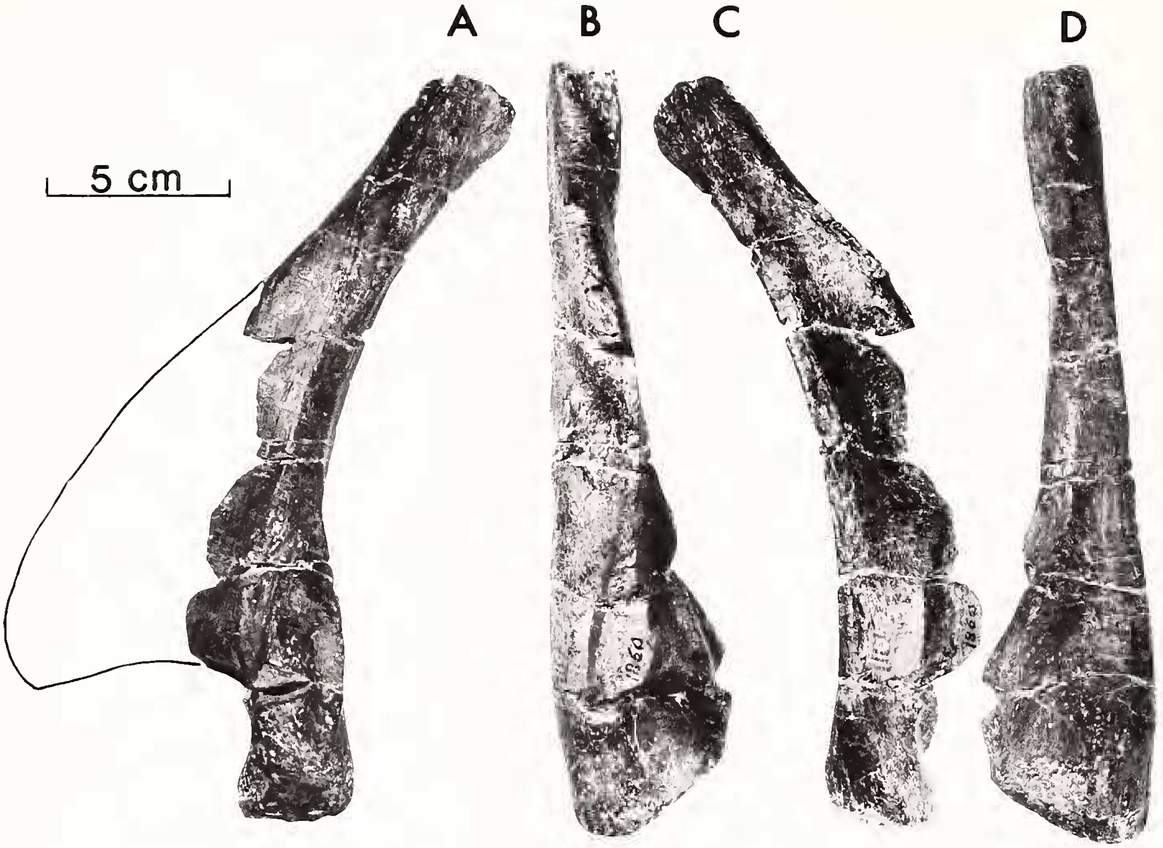

Fig. 10.—A, lateral, B, anterior, C, medial, and D, posterior views of left quadrate probably belonging to the holotype of *Apatosaurus ajax* YPM 1860. Missing anterior pterygoid process indicated in A. Distal end toward bottom.

anterior surface of the shaft is excavated into a shallow depression, giving the articular surface a kidney-shaped outline. In anterior view the condylar surface slopes ventromedially.

In Marsh's (1896) description of the cranium from Morrison, Colorado, as "*Atlantosaurus montanus*" the only feature he commented on was a so-called pituitary canal leading from the brain cavity down through the base of the skull. The cranium was illustrated by Marsh (1896:274, Pl. XV) in posterior and ventral views only and with just a few of the sutures and foramina indicated; further preparation has revealed almost all of these features clearly (Fig. 11). The only major portions of the occiput not represented are the distal end and superior margin of the lateral, occipital wing of the parietal, and the occipital process of the squamosal that forms the lateral border of the posttemporal fossa. Only the left side of the cranial roof is present but this includes most of the parietal and frontal, and the posterior third of the prefrontal. The parietal-frontal juncture has been destroyed, separating the cranial roof from the principal portion of the cranium; these have been reunited in what is thought to be their correct relative position. The more complete left cranial wall includes the exoccipital-opisthotic complex, proötic, laterosphenoid, and the base of the orbitosphenoid. Of the cranial floor elements, the basioccipital is complete, the basisphenoid lacks mainly the basipterygoid processes and the parasphenoidal rostrum is broken off at its base. The occipital condyle is as in *Diplodocus* in its shape and orientation and the skull must have been directed at nearly a right angle to the neck. The basioccipital-basisphenoid suture is not detectable. Two features of the cranial roof clearly distinguish the cranium from that of *Camarasaurus* and give it a distinctly *Diplodocus*-like character: 1) the posterior end of the prefrontal is triangular and projects posteromedially into the anterolateral corner of the frontal, and 2) a moderately deep, concave emargination of the orbital margin of the frontal occurs

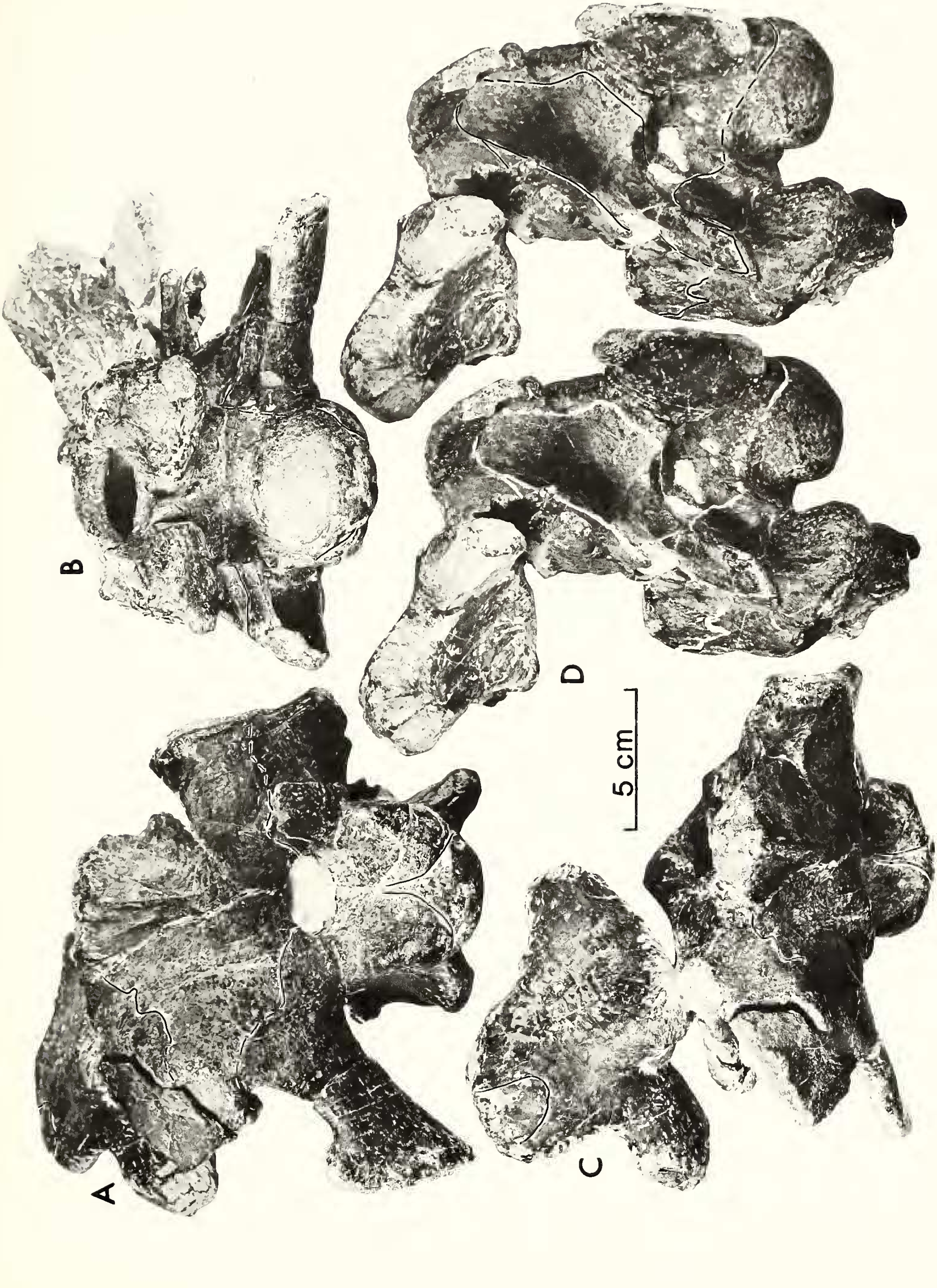

Fig. 11.—A. posterior, B. ventral, C. dorsal, and D. left lateral (stereo pair) views of braincase probably belonging to holotype of *Apatosaurus ajax* YPM 1860.

at a level just behind the posterior end of the prefrontal. Both these features are present in the probable *Apatosaurus* skull CM 11162. Only a few minor differences between the Morrison cranium and that of *Diplodocus* can be noted. Small proportional differences, such as the greater size of the condyle and basal tubercles, are to be expected in the Morrison cranium because of the greater robustness of *Apatosaurus* over *Diplodocus*. The proötic-laterosphenoid suture is tightly closed and is not an abutment contact as in *Diplodocus;* this probably indicates a fully grown individual. The transverse opening of the "pituitary canal" between the basal tubercles that was noted by Marsh (1896) is most likely the result of incomplete preservation. The thin cranial floor in this region and the fact that the cranium was glued along a number of breaks that intersect this opening could account for the absence of bone here.

One other piece of evidence suggests that the skull of *Apatosaurus* was like that of *Diplodocus*. Examination of the partial skeletons field nos. 24 (CM 3390) and 37, found about 6 m apart at Dinosaur National Monument (Fig. 1), convinces us that Douglass (see Historical Review) was probably correct in his conclusion that these specimens belong to the same juvenile individual of *Apatosaurus*. Unfortunately, although the anterior portion of a small jaw possessing *Diplodocus*-like teeth (field no. 35) that was noted by Douglass in the collection records as having been found with field no. 37 was prepared at the Carnegie Museum, it cannot be located. If Douglass' observation on the nature of the teeth of the jaw is correct—there is no reason to doubt it—and if the jaw and field specimens nos. 24 and 37 were part of one individual, then it follows that *Apatosaurus* had *Diplodocus*-like teeth, reinforcing our conclusion that the skull of *Apatosaurus* is *Diplodocus*-like.

## COMPARISON OF POSTCRANIAL SKELETONS

If *Apatosaurus* possessed a *Diplodocus*-like, rather than a *Camarasaurus*-like, skull, it may be asked how the postcranial skeletons of these three sauropods compare. Comparisons are made possible by detailed accounts of the postcranial skeletons of *Diplodocus* (Osborn, 1899; Hatcher, 1901*a*, 1902; Holland, 1906; Gilmore, 1932), *Apatosaurus* (Gilmore, 1936), and *Camarasaurus* (Gilmore, 1925). The postcranial skeletons of *Apatosaurus* and *Camarasaurus* have been generally considered more similar to each other than to *Diplodocus* because of their much greater robustness. It is in fact difficult to distinguish between isolated hindlimb bones of *Apatosaurus* and *Camarasaurus*, especially if these elements are imperfectly preserved. Excepting this superficial resemblance between *Camarasaurus* and *Apatosaurus*, the postcranial skeletons of *Apatosaurus* and *Diplodocus* share a large number of characters that set them widely apart from *Camarasaurus*. *Diplodocus* and *Apatosaurus*, in contrast to *Camarasaurus*, have relatively very long necks, short trunks, and very long tails, unusual anterior caudal vertebrae and midcaudal chevrons, shorter forelimbs and metacarpals, and reduced number of carpal and tarsal elements.

### VERTEBRAL COLUMN

The cervical vertebrae, particularly the posterior ones, are among the most diagnostic bones in the sauropod skeleton. *Apatosaurus* and *Diplodocus* possess 15 cervicals, *Camarasaurus*, 12. In all three genera the neural spines of the posterior cervicals and the anterior dorsals are deeply cleft; in *Apatosaurus* and *Diplodocus* the clefts are V-shaped, whereas those of *Camarasaurus* are more U-shaped. The cervicals of *Apatosaurus* are proportionally shorter and more solidly constructed than those of either *Diplodocus* or *Camarasaurus*. In *Apatosaurus* and *Diplodocus* the cervical ribs are much shorter than in *Camarasaurus* and do not extend beyond the posterior end of the centrum from which they originate, whereas in *Camarasaurus* some cervical ribs, such as the ninth, may reach a length of about two and a half times the length of the centrum. The cervical ribs of *Apatosaurus* are considerably stouter than those of either *Diplodocus* or *Camarasaurus*. *Apatosaurus* and *Diplodocus* have 10 dorsal vertebrae that exhibit similar regional variations. Their anterior dorsal centra are opisthocoelous; posteriorly they are amphiplatyan or amphicoelous. In the shoulder region the neural spines in both are low but rise posteriorly to become very high and slender in the sacral region. *Camarasaurus* has 12 dorsals, all of which are opisthocoelous. The dorsal neural spines exhibit little change in height posteriorly and at the posterior end of the series they are much lower, stouter, and laterally expanded above than in the other two genera.

There are five sacral vertebrae in all three genera. In *Apatosaurus* and *Diplodocus*, the sacral centra and ribs are hollow, the second and third spines are united and there is a tendency for the fourth to unite with the third. In *Camarasaurus* the centra are solid or have much smaller cavities and four or even all five spines may fuse.

The tails in *Apatosaurus* and *Diplodocus* reach enormous lengths, up to 82 caudals in the former and 73 or more in the latter; the caudals of approximately the posterior third of their tails consist essentially of elongated rods that form a "whip-lash" structure. The centra in both are generally amphiplatyan throughout, although there is a tendency, particularly in *Diplodocus*, for the anterior centra to be somewhat procoelous. In both genera the transverse processes in the anterior part of the tail form thin, vertically expanded, wing-like plates that more closely resemble the sacral ribs than the transverse processes of the remainder of the tail. In *Apatosaurus* the first three or four caudals show this development; in *Diplodocus* it occurs in the first 12 or more. In both the caudal spines are very high anteriorly and their distal ends are not expanded transversely. Their anterior caudal chevrons are of normal structure, the laminae of the chevrons being united by a bridge of bone above the haemal canal but joining below the canal to form a simple, laterally flattened spine. The chevrons of the mid-caudal region, however, are unusual in that they lack the bridge of bone above the haemal canal and the laminae do not unite immediately below the canal but at the ends of well-developed anteriorly and posteriorly directed processes that originate at their distal ends. This character is more pronounced in *Diplodocus*. The presence of these unusual mid-caudal chevrons in *Apatosaurus* was not discussed by Gilmore (1936) because only the anterior three chevrons are present in the specimen (CM 3018) studied by him, but he did indicate them in his post-cranial restoration. The "double-arch" type of mid-caudal chevron was, however, briefly noted by Riggs (1903*b*) and shown in his restoration of *Apatosaurus*. In some features the caudals of *Apatosaurus* and *Diplodocus* are distinct. The anterior caudal centra of *Diplodocus* have deep lateral pleurocoels and ventral excavations; the ventral excavations occur well into the midcaudal region. The centra are even more elongated in *Diplodocus* than in *Apatosaurus*, a feature which becomes more pronounced posteriorly, especially in the whip-lash portion of the tail. In *Apatosaurus* the caudal centra are not excavated laterally or ventrally except for possibly the first few, which may have small irregularly placed cavities, and the anterior centra have a blunt, ventral keel. The tail of *Camarasaurus* differs from those of *Apatosaurus* and *Diplodocus* in having only 53 much shorter vertebrae. The transverse processes of even the anteriormost caudals are simple. The anterior neural spines are not unusually high and distally are expanded transversely into ball-like structures. The centra are amphicoelous, unexcavated and without a ventral keel, and the chevrons are unspecialized throughout and almost never enclose the haemal canal above.

### APPENDICULAR SKELETON

The marked difference in massiveness of the appendicular skeletons of *Diplodocus* and *Apatosaurus* is more apparent than their similarities. The scapulae are distinct in all three genera. The broad plate, which extends anterodorsally from the base of the scapular blade, is more vertically expanded and the prominent ridge, which divides its external surface into two broad muscle fossae, is less developed and makes a larger angle with the shaft in *Apatosaurus* and *Camarasaurus* than in *Diplodocus*. The upper end of the scapula is greatly expanded in *Camarasaurus*, much less so in *Diplodocus*, and only slightly expanded in *Apatosaurus*. The coracoids are dissimilar in outline in all three, being quadrangular in *Apatosaurus*, roughly triangular in *Camarasaurus*, and intermediate between these two in *Diplodocus*. The ilia in all three genera are similar. The pubes of *Apatosaurus* and *Diplodocus* are relatively slender compared to those of *Camarasaurus*. *Diplodocus* has a pronounced hook-like process for the ambiens muscle on the upper, anterior margin of the pubis; this process is much less prominent in *Apatosaurus* and is nearly absent in *Camarasaurus*. Confusion has occurred through the legend of figure 37 in Gilmore's (1936) description of *Apatosaurus* in which the figured pubis of *Diplodocus carnegiei* CM 94, exhibiting a very prominent ambiens process, is mistakenly identified as *Apatosaurus excelsus* CM 563. The figure given by Hatcher (1903*a*, Pl. IV, Fig. 1) of the pelvis of CM 563 also tends to exaggerate this feature in *Apatosaurus*. The ischium is one of the most diagnostic bones in the sauropod skeleton. In *Apatosaurus* and *Diplodocus* the blades of the ischia are tilted ventromedially and their expanded distal ends contact each other along a wide margin of the ventral borders of their medial surfaces. The more slender blades of the ischia in *Camarasaurus* are not expanded distally and are twisted along their long axes so that the ends of the blades come to lie in a horizontal plane with their inferior margins contacting each other medially.

Perhaps the most striking and significant feature separating the limbs of *Apatosaurus* and *Diplodocus* from those of *Camarasaurus* is their forelimb to hindlimb length ratio; the humerofemoral length ratio is 2/3 in both *Apatosaurus* and *Diplodocus* and 4/5 in *Camarasaurus*. The forelimb of *Apatosaurus* is robust, rivaled in this feature only by that of the South American *Titanosaurus australis* (von Huene, 1929). Forelimbs of *Camaraurus* resemble those of *Diplodocus* more nearly in their overall slenderness, although the humerus of *Camarasaurus* is somewhat more robust and the medially projecting process at the upper end of its ulna is also more pronounced. The manus of *Apatosaurus* and *Diplodocus* are similar so far as known. A single carpal bone remains in *Apatosaurus*; the condition in *Diplodocus* is unknown. The metacarpals of *Apatosaurus* are short and robust and in *Diplodocus* they are short but more slender. *Camarasaurus* has two carpals and its metacarpals are very long and slender. The hindlimb bones of *Apatosaurus* and *Camarasaurus* are about equal in their much greater robustness than those of *Diplodocus*. Despite this feature, the hindlimbs of *Apatosaurus* and *Diplodocus* can be distinguished from those of *Camarasaurus*. The femur of *Camarasaurus* has a straight shaft, whereas femora of *Apatosaurus* and particularly of *Diplodocus* exhibit a slight sigmoid curve. In *Camarasaurus* the cnemial crest of the tibia is relatively less pronounced and the muscle scar on the lateral surface of the fibula is much more strongly developed than in the other two genera. The pes of *Apatosaurus* and *Diplodocus* exhibit differences from that of *Camarasaurus*. No calcaneum has yet been found associated with any *Diplodocus* or *Apatosaurus* pes, and, although the question of its existence has not been settled, the evidence strongly suggests that the only tarsal element they possess is an astragalus. In *Camarasaurus* the tarsus consists of an astragalus and a small, spherical calcaneum. The metatarsals of *Apatosaurus* and *Diplodocus* are very similar except that the third and fourth are more slender in the latter. In both, metatarsals III and IV are the longest, the fourth often being slightly longer, and metatarsal I is unusual in having a process on the posteroventral margin of its lateral surface. In *Camarasaurus* metatarsals II and III are equal in length and the longest, and metatarsal I does not possess the above-mentioned process.

## RELATIONSHIPS OF *APATOSAURUS*

It has become common practice (Janensch, 1935; Nopcsa, 1930; von Huene, 1948) to divide the Sauropoda into two families primarily on the basis of dentition. Though a variety of family names has been employed, these classifications are in essential agreement in their separation of the broad, spatulate-toothed forms such as *Brachiosaurus* and *Camarasaurus* from the slender-toothed forms such as *Diplodocus*. The long-standing conclusion that *Apatosaurus* had a *Camarasaurus*-like skull and dentition was the major reason for its alliance with the former group. Romer (1956) divided the sauropods into the Brachiosauridae and Titanosauridae; *Apatosaurus* was assigned to the latter family even though Nopcsa (1930) and von Huene (1948) placed it in the former. White (1958), believing he had substantiating evidence that the skull of *Apatosaurus* was *Camarasaurus*-like, recommended the removal of *Apatosaurus* from the Titanosauridae and placement in the subfamily Camarasaurinae of the Brachiosauridae. In a later classification Romer (1966) referred *Apatosaurus* to the Titanosauridae and *Brontosaurus* to the Brachiosauridae even though Riggs (1930*b*) had clearly demonstrated that the latter genus is a junior synonym of the former. It is beyond the scope of this paper to present a revised classification of the sauropods, but we reject the commonly used, two-family division, which artificially associates widely divergent forms.

*Apatosaurus* and *Diplodocus* are morphologically very similar, and the former is quite different from *Camarasaurus*, to which it has been closely allied by many authors. Equally important, *Apatosaurus* and *Diplodocus* share a suite of characters that can be seen in various combinations in five other less well known sauropod genera—*Barosaurus, Cetiosauriscus, Mamenchisaurus, Dicraeosaurus,* and *Nemegtosaurus*. These genera are judged by us to be very closely related and quite distinct from all other adequately known sauropods and deserving of familial separation. The oldest valid name available for this group is Diplodocidae Marsh (1884).

The only other family names that could be considered, Atlantosauridae (Marsh, 1877*b*) and Amphicoeliidae Cope (1877*b*) are rejected because their type genera are indeterminate. In the case of Atlantosauridae the type genus *Atlantosaurus* (first described as *Titanosaurus* Marsh, 1877*a*) cannot be adequately defined and has to be considered a *nomen dubium*. The type species, *A. montanus*, is based on only an incomplete sacrum (YPM 1835) that cannot be clearly distinguished from those of a number of sauropods, including genera outside the new family grouping proposed here. The adoption of Amphicoeliidae has the same drawback as Atlantosauridae; the type genus cannot be adequately defined. The family was established by Cope (1877*b*) to include two species of a new genus, *Amphicoelias altus*, the type species, and *A. latus;* a third species, *A. fragillimus,* was later added by Cope (1878*b*). In a restudy of these species, all of which are represented by single specimens, Osborn and Mook (1921) concluded that *A. altus* represents a young individual of *Camarasaurus* and suggested that *A. fragillimus* should be provisionally referred to *A. altus;* we are in agreement with these conclusions. Though the type of *A. altus* is referable to the Diplodocidae, as defined below, its incompleteness does not allow it to be distinguished from either *Diplodocus* or *Barosaurus*. *Diplodocus* was first described by Marsh (1878*b*) on the basis of a small, but adequately diagnostic portion of the postcranial skeleton, yet it was not until his later description of the skull (1884) that he considered the genus unique and the type of a new monotypic family, Diplodocidae. Though Marsh (1898) later transferred *Barosaurus* from the Atlantosauridae to the Diplodocidae, subsequent classifications of the sauropods by von Huene (1927*a*, 1927*b*) continued to recognize the latter family as monotypic. In a recent catalogue of the dinosaur genera White (1973), without giving a revised or expanded definition of the family Diplodocidae, included within it a great variety of genera, many of which are too divergent to be grouped together at this taxonomic level.

The availability of the family name Diplodocidae is fortunate because *Diplodocus* is well known and very representative of the new family grouping proposed here, for which we offer the following revised definition.

### **Diplodocidae**, Marsh, 1884

*Definition*.—SKULL: nares superior in position; quadrate directed anteroventrally; basipterygoid processes elongated; definition of weak, pencil-like teeth. VERTEBRAL COLUMN: midpresacrals exhibit tendency toward "cervicalization" to produce long neck; midpresacral spines cleft; sacral spines very high; anterior caudals with broad, wing-like transverse processes; midcaudal chevrons having distal, fore and aft directed processes; tail consisting of large number of vertebrae, forming a "whip-lash" structure. APPENDICULAR SKELETON: Forelimbs short with a humerofemoral length ratio of 2/3; tarsus and at least in some cases the carpus reduced to single element; distal ends of ischia expanded in vertical plane and contacting each other along a wide, ventral margin of their medial surfaces; process on posteroventral edge of lateral face of metatarsal I; metatarsals III and particularly IV longest.

*Remarks*.—Although our inclusion of *Apatosaurus* in the Diplodocidae is obvious, assignment of the other genera to this family must be justified. The brief comments that follow are intended to serve this purpose.

The Upper Jurassic *Barosaurus* Marsh, 1890, is structurally very close to *Diplodocus* and is distinguished mainly by its enormously elongated cervical vertebrae and slightly less developed caudal neural arches and spines; its limb elements are scarcely distinguishable from those of *Diplodocus*. In *Barosaurus* cervicalization of the midpresacrals is evident, the anterior caudals have wing-like transverse processes, the midcaudal chevrons possess the *Diplodocus*-like fore and aft processes, the distal ends of the ischia are expanded and contact each other on their ventromedial surfaces, and metatarsal I has a distinct process on the posteroventral edge of its lateral surface.

*Cetiosauriscus* von Huene (1927*b*) has not previously been associated with the members of the family group proposed here, but a number of characters indicate that this Upper Jurassic genus should be considered a primitive member of the Diplodocidae. Except for several posterior dorsal centra, its presacral vertebrae, which are very diagnostic among the sauropods, are otherwise unknown. The anterior caudals, although incompletely known, appear to possess wing-like transverse processes, the midcaudal chevrons are *Diplodocus*-like in that their distal ends possess fore and aft directed processes and there is a whip-lash development of the tail. The humerofemoral length ratio is 2/3. The calcaneum appears to be absent in the tarsus and the astragalus is the only tarsal element. Metatarsals III and IV are the longest and metatarsal I clearly exhibits a process on the posteroventral margin of its lateral surface.

The Upper Jurassic *Mamenchisaurus* Young, 1954, tentatively referred to Diplodocidae, has a long neck with 19 cervicals and there are 11 dorsal vertebrae, which possess cleft neural spines. The length of the tail is unknown, but the midcaudal chevrons possess the distal fore and aft directed processes as in *Diplodocus*. Though the humerus and femur are not known for any one specimen, the humerofemoral length ratio is considered to be a little greater than 2/3 in the type genus. This is based on the fact that the height of the sacral neural spines is relatively somewhat less than in other members of the family and that there exists a direct correlation between the height of the sacral spines and the humerofemoral length ratio. This ratio may vary among specimens referred to this genus and only articulated material will reveal its true value.

*Dicraeosaurus* Janensch, 1914, is a somewhat puzzling, Upper Jurassic genus and is tentatively referred to this family. The neck is short; the number of both the cervical and dorsal vertebrae is 12. Surprisingly, the dorsal vertebrae do not possess pleurocentral cavities; the skull and teeth, however, are distinctly diplodocid. The neural spines of the presacrals are more deeply cleft than in any other sauropod and the sacral spines are high. The anterior caudals have wing-like, transverse processes and the midcaudal chevrons are *Diplodocus*-like. The distal ends of the ischia are greatly expanded. The forelimb is short, which, along with the high sacral spines, suggests that the humerofemoral length ratio may be close to 2/3.

Finally, the Upper Cretaceous *Nemegtosaurus* Nowinski, 1971, known only by the skull, which is distinctly diplodocid in structure, including the teeth, is referred to Diplodocidae.

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